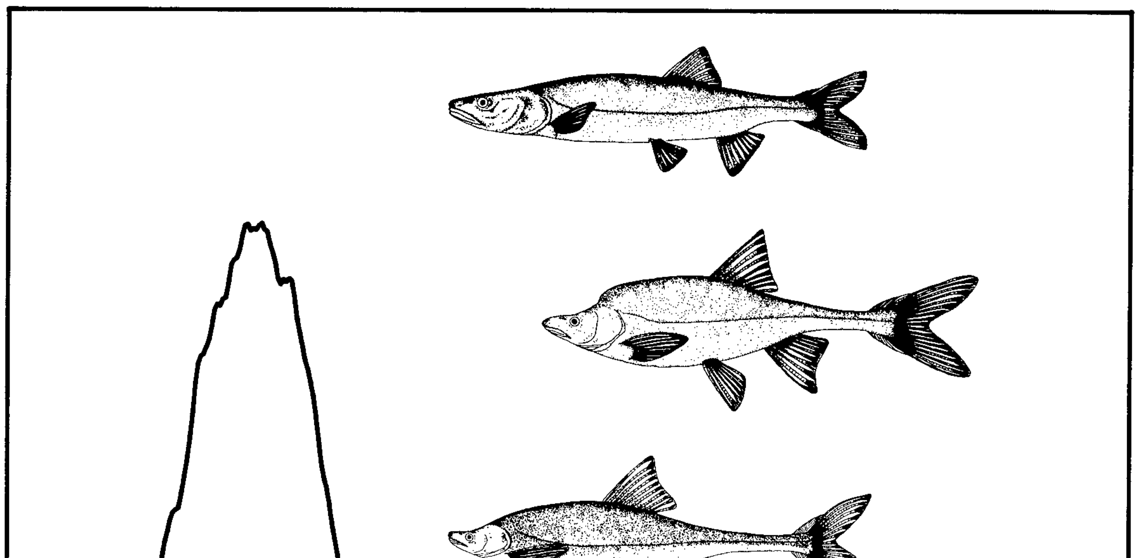
Biological Report 89(14)
July 1989

Habitat Use and Streamflow Needs of Rare and Endangered Fishes, Yampa River, Colorado



Fish and Wildlife Service
U.S. Department of the Interior

Biological Report

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Cover: Colorado squawfish, humpback chub, bonytail chub, and razorback sucker shown with the average annual streamflow, Yampa River. *Fish illustrations by James M. Beard.*

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Habitat Use and Streamflow Needs of Rare and Endangered Fishes, Yampa River, Colorado

by

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Contents

Preface

The decline of the native Colorado River fish fauna is a biological indicator of dramatic environmental change and the potential loss of a unique natural resource. This decline is associated with human population expansion and associated water development in the West, limited interest in nongame fish biology, and a lack of a conservation ethic for fishes of western deserts. For these and other reasons, management and recovery options have been difficult to develop for rare fishes in the Colorado River basin. Only recently have substantive life cycle and habitat use information of these fishes become available and their requirement for large and diverse habitats been recognized.

Flow and nonflow management measures for the rare Colorado River fishes are currently being developed based on provisions inherent in Section 7 of the Endangered Species Act. Since passage of that Act in 1973, the proliferation of literature and symposia concerning recovery of the Colorado River fishes reflects the keen interest in their management and recovery.

Major conflicts between various water development groups, the U.S. Fish and Wildlife Service, and others regarding the cumulative effects of water development projects on recovery of the rare fishes led to the formation of the multiagency Upper Colorado River Basin Coordinating Committee in 1984. Active participants include the U.S. Fish and Wildlife Service; U.S. Bureau of Reclamation; States of Colorado, Utah, and Wyoming; private water development interests; and environmental groups. Cooperation of these diverse interests demonstrates the complexity involved in recovery of the rare Colorado River fishes.

In 1987 the Upper Colorado River Basin Coordinating Committee produced a Recovery Implementation Program for recovering the rare fishes of the upper Colorado River basin. The ultimate goal of this program was to recover and delist the Colorado squawfish (*Ptychocheilus lucius*), humpback chub (*Gila cypha*), and bonytail chub (*G. elegans*). In addition, management options would be developed for the razorback sucker (*Xyrauchen texanus*) so that protection under the Endangered Species Act would not be needed.

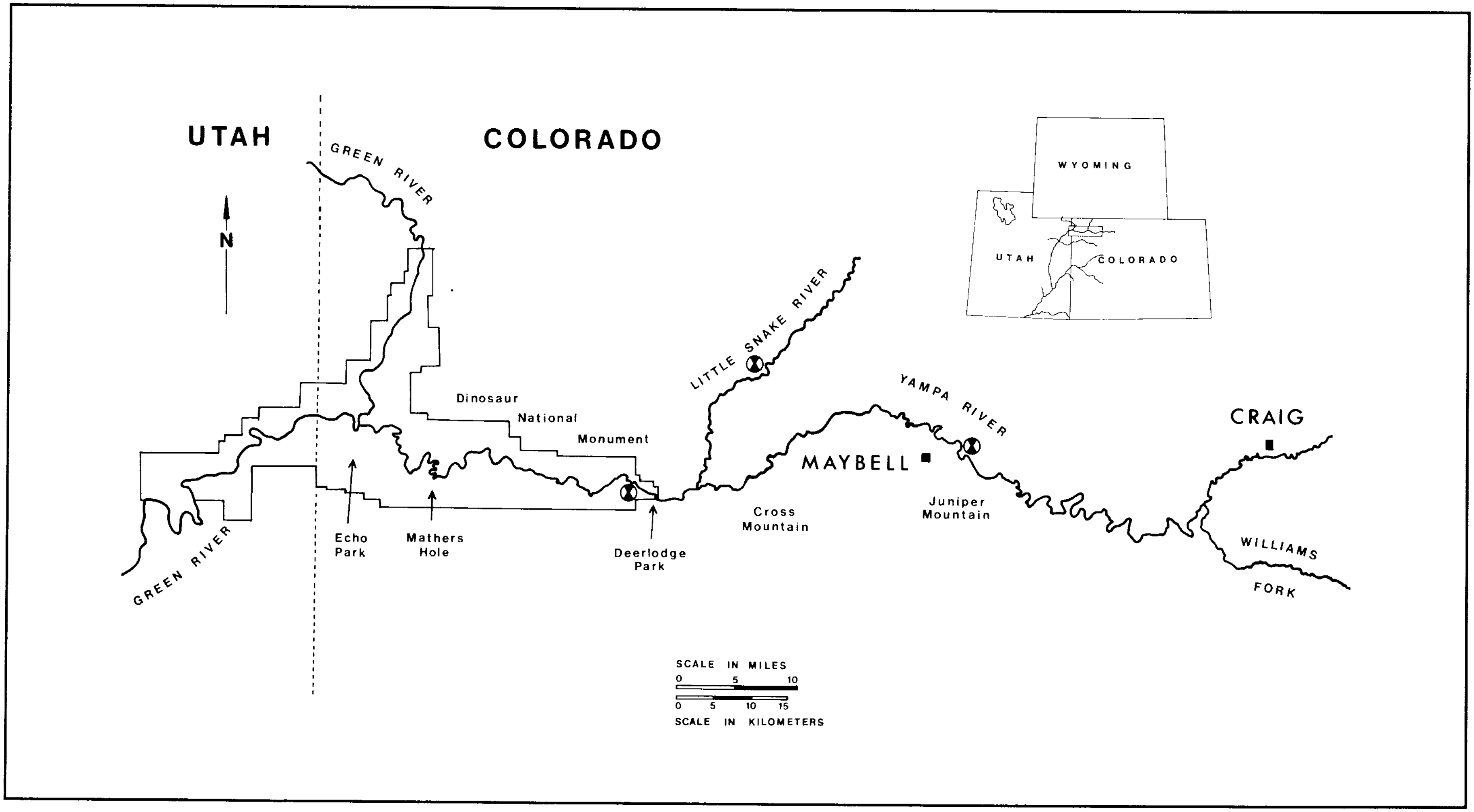
One element of the Recovery Implementation Program is the protection of streamflow needs of the listed fishes. In meeting this goal, the Yampa River has been assigned highest-priority for water rights acquisition. As the only large river in the upper Colorado River basin in which flow patterns have not been substantially altered by water development projects, the Yampa River is considered important for the maintenance and recovery of existing populations of rare Colorado River fishes.

In 1988, the Upper Colorado River Basin Coordinating Committee requested that streamflow requirements of the rare fishes in the Yampa River be quantified to aid water acquisition in line with the goals of the Recovery Implementation Program. A two-step process was subsequently outlined: (1) evaluation of habitat use, potential limiting factors, and general flow needs (i.e., relation between life cycle and annual flow events) of the four fish species; and (2) quantification of the identified needs with respect to quantity, duration, and timing of flows. The present report fulfills step 1: it is an evaluation of habitat use and streamflow requirements of the Colorado squawfish, humpback chub, bonytail chub, and razorback sucker in the Yampa River.

Questions regarding technical material in this report may be addressed to the authors. Additional information regarding the Recovery Implementation Program may be obtained from Colorado River Coordinator (FWE), U.S. Fish and Wildlife Service, P.O. Box 25486, Denver Federal Center, Denver, Colorado 80225.

Acknowledgments

This report was made possible by the research of many investigators, many of whom we cite, all of whom we hereby acknowledge. The U.S. Bureau of Reclamation, U.S. Fish and Wildlife Service, U.S. National Park Service, U.S. Bureau of Land Management, and U.S. Congress provided funds and support. Colorado Division of Wildlife and U.S. Fish and Wildlife Service biologists cooperated in collection of field data. J. Hamill and L. Mills furnished administrative support and guidance in the inception and formulation of the manuscript. B. Haines, N. Nikirk, and K. Paulin assisted with data analyses and graphics. M. Butler, R. Peterson, and G. Smith provided hydrological information and assistance. D. Hann, S. Lanigan, W. Minckley, K. Rose, and R. Wydoski improved the draft manuscript. Lastly, members of the Technical Group of the Upper Colorado River Basin Coordinating Committee approved funding for this report and provided comments for preparation of the final manuscript.



Yampa River study area, confluence with the Green River at Echo Park to Craig, Colorado (river kilometer 0–224). = locations of USGS river gauges.

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Introduction

The Yampa River – largest tributary to the Green River – is located in northwestern Colorado and southern Wyoming (see map opposite page). From its headwaters on the western slope of the Rocky Mountains (about 3,780 m above sea level; see appendix for measurement conversions), the Yampa River meanders northward and then westward to Craig, Colorado (river kilometer [RK] 224). It then passes through low-gradient agricultural valleys and enters the canyons of Juniper Mountain (RK 145.6–141.9) and Cross Mountain (RK 94.1–88.9). Downstream of the Little Snake River confluence (RK 81.6), the Yampa River enters Dinosaur National Monument (DNM) and the Yampa Canyon (Deerlodge Park to Echo Park, RK 75.2–0), where it becomes a higher-gradient system of rocky runs and rapids. The gradient again becomes more moderate below Big Joe Rapid (RK 38.4), and the Yampa River deepens and becomes relatively slow-moving through the incised meanders of Mathers Hole (RK 28.3). After a short drop at Warm Springs (RK 6.4), the Yampa River enters the Green River at Echo Park, DNM (about 1,524 m above sea level). Thus, the mainstream Yampa River is composed of relatively high-gradient canyon reaches dominated by boulder, cobble and gravel substrates, and low-gradient reaches of meandering canyon and flat, open terrains dominated by finer substrates. The Yampa River flows about 320 km and drops in elevation about 2,256 m (Joseph et al. 1977).

Average annual discharge of the Yampa River is about 60.5 m^3/s, of which about 28% is contributed by the Little Snake River (sum of United States Geological Survey [USGS] flow records for Yampa River near Maybell, Colorado, and Little Snake River near Lily, Colorado, for 1922–87, M. Butler, written communication). Flows begin to rise in the Yampa River in late March due to spring runoff and remain high through July (Fig. 1). Mean flow during spring runoff in the Yampa River is about 153.18 m^3/s (USGS flow records). River level may undergo large fluctuations during spring runoff due to local warming trends and flash floods. Although floods are of short duration, peak flows can be high. A maximum discharge of 939.56 m^3/s was recorded 18 May 1984 in the Yampa River at Deerlodge Park (Ugland et al. 1987). Following spring runoff, flows of the Yampa River decline toward a monthly base flow of about 14.15 m^3/s for August through March (USGS flow records), and large fluctuations in river level are infrequent events. Thus, fishes indigenous to the Yampa River evolved in a system of fluctuating seasonal and annual flows characterized by wet, average, and dry climatic periods. We consider the recurring cycle of high spring flows followed by a period of lower flows (Fig. 1) the natural or current flow regime of the Yampa River. This regime is typically a system of fluctuating low, average, and high flow years.

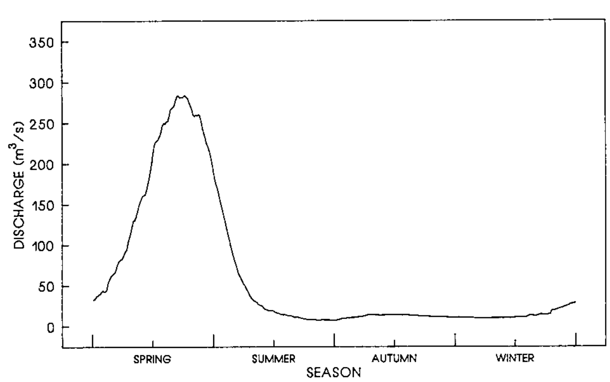

Fig. 1. Average annual distribution hydrograph, Yampa River, 1922–87.

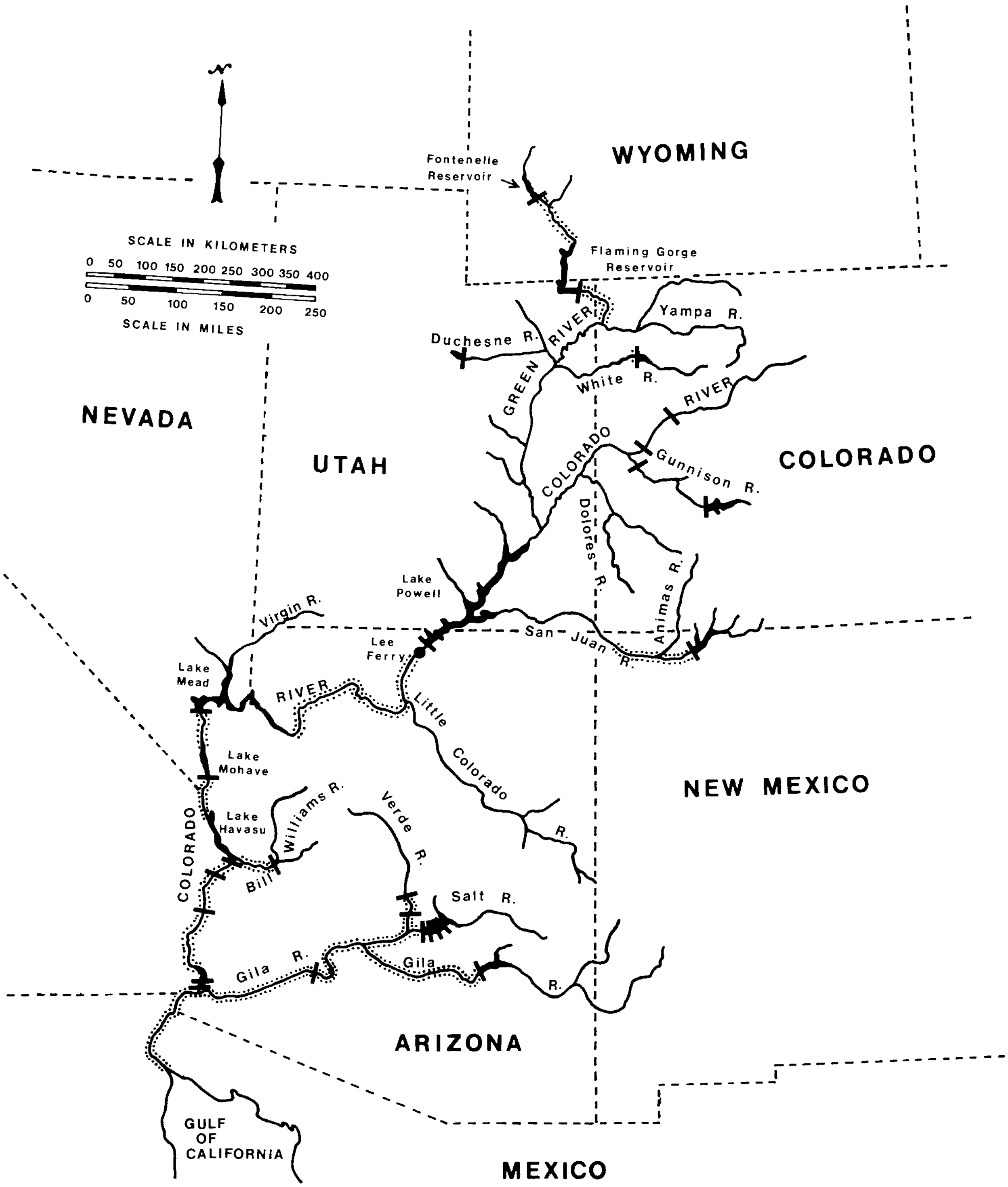

Fig. 2. Mainstream barriers and their impacts in the Colorado River basin (after Tyus 1984). **||** = location of barrier; ⁞⁞ = downstream impact; and *blackened areas* = impoundments due to project completion.

The Yampa River is the only large river in the Colorado River basin in which flow patterns have not been substantially altered by water development projects (Fig. 2). Examples of downstream alterations include modification of flow and temperature patterns, and channel morphology. Upstream loss of fish habitat can occur with stream blockage and impoundment. Construction of the Flaming Gorge and Fontenelle dams on the Green River in the 1960's eliminated spring peak flows and increased baseline discharge in that system. However, the spring and early summer peak in the existing Green River hydrograph below the confluence of the Yampa River is maintained by spring runoff from the Yampa River (Fig. 3).

Fishes indigenous to the Yampa River include cyprinids (Colorado squawfish [*Ptychocheilus lucius*], humpback chub [*Gila cypha*], bonytail chub [*G. elegans*], roundtail chub [*Gila robusta*], speckled dace [*Rhinichthys osculus*]); catostomids (razorback sucker [*Xyrauchen texanus*], flannelmouth sucker [*Catostomus latipinnis*], bluehead sucker [*C. discobolus*], mountain sucker [*C. platyrhynchus*]); salmonids (Colorado River cutthroat trout [*Salmo clarki pleuriticus*]; Rocky Mountain whitefish [*Prosopium williamsoni*]); and sculpins (*Cottus bairdi* sp.; Tyus et al. 1982a; Behnke and Benson 1983; Woodling 1985). All mainstream fishes persist today despite the introduction of at least 18 nonnative fishes (Tyus et al. 1982a; Wick et al. 1985; U.S. Fish and Wildlife Service, unpublished data). Native fishes also dominate the Yampa River fish community as indicated by Miller et al. (1982) and Wick et al. (1985). Using electrofishing and trammel netting techniques, these investigators found that native fishes composed more than 70% of the catch, and Miller et al. (1982) reported that 54% of all fishes captured (including collections of small fishes) were native. Persistence of native fishes is most often observed in unaltered (natural) river systems (e.g., Yampa River and Little Colorado River) and is presumably associated with maintenance of usable fish habitat due to a regimen of fluctuating seasonal and annual flows.

Historically, the native cyprinids and catostomids were the dominant fishes in mainstream habitats of the Colorado River basin. The Colorado squawfish, bonytail chub, humpback chub, and razorback sucker were widely distributed and common-to-abundant in major rivers of the Colorado River basin. However, all four species are now threatened with extinction due to the combined effects of habitat loss; regulation of natural flow, temperature, and sediment regimes; proliferation of introduced competitors and predators; and other man-induced disturbances (Miller 1961; Minckley 1973; U.S. Fish and Wildlife Service 1987). The Colorado squawfish, humpback chub, and bonytail chub are federally protected as endangered species under provisions of the Endangered Species Act of 1973 (U.S. Fish and Wildlife Service 1986). The razorback sucker, a candidate species for Federal listing, is protected by State statutes in Arizona, California, Colorado, Nevada, and Utah (U.S. Fish and Wildlife Service 1985, 1987).

In the lower Colorado River basin (below Lee Ferry, Arizona), the Colorado squawfish has been extirpated; relict populations of bonytail chub and razorback sucker remain in some impoundments; and the humpback chub persists only in the Little Colorado River (Minckley 1973, 1983). In the upper Colorado River basin, the

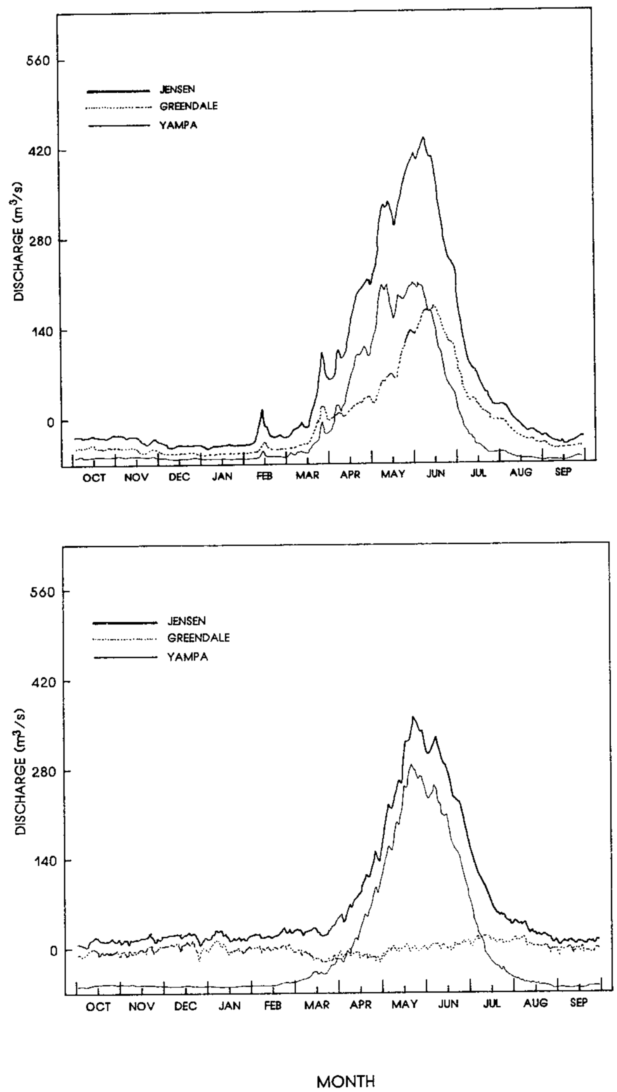

Fig. 3. Average annual distribution hydrograph for the Green and Yampa rivers. Upper figure for 1951–62; lower figure for 1964–84. USGS flow records: *Jensen* = Green River at Jensen, Utah; *Greendale* = Green River below Flaming Gorge Dam; *Yampa* = Yampa River at mouth (Yampa River near Maybell, Colorado, and Little Snake River near Lily, Colorado).

Colorado squawfish persists in the Yampa and Green rivers, the upper Colorado River mainstream, and the lower San Juan River (Archer et al. 1985; Tyus et al. 1987; Meyer and Moretti 1988; Tyus 1989). The humpback chub is presently self-sustaining in the Yampa River and upper Colorado River (Archer et al. 1985; Karp and Tyus 1989). The razorback sucker persists in the lower Yampa and Green rivers, the mainstream Colorado River, and the lower San Juan River, but there is little indication of recruitment in these remnant populations (Tyus et al. 1986; Meyer and Moretti 1988; Lanigan and Tyus 1989; Tyus 1989). The bonytail chub is extremely rare in the upper Colorado River basin (Valdez and Clemmer 1982; U.S. Fish and Wildlife Service 1987). All four fishes have been extirpated in the Green River between Flaming Gorge Dam and the Yampa River confluence, due to loss of usable habitat following closure of the dam (Vanicek et al. 1970). However, the Yampa River supports all its native fish fauna (including self-sustaining populations of some of the rare species), contains much rare fish habitat, and contributes to the maintenance and availability of usable rare fish habitat in the downstream Green River.

Our objective is to evaluate habitat use and streamflow needs of Colorado squawfish, bonytail chub, humpback chub, and razorback sucker in the Yampa River. Habitat requirements and factors limiting the distribution and abundance of each species are discussed by life history stage. Flow events considered essential to the survival of these four fishes in the Green River basin are identified for further quantification. Our intent is to describe flow needs of Colorado squawfish, bonytail and humpback chubs, and razorback sucker as indicated by their habitat use. We do not provide a quantification of these needs.

Distribution, Abundance, and Habitat Use

The distribution and abundance of fishes indigenous to the Yampa River have been studied since the early 1900's (Ellis 1914; Beckman 1952; Banks 1964; Vanicek et al. 1970; Holden and Stalnaker 1975). Early field studies provided much baseline information, although they were generally restricted in scope to seasonal fish surveys. More intensive, long-term sampling programs in the 1970's and 1980's (Prewitt et al. 1977; Seethaler 1978; Wick et al. 1979, 1982, 1985; McAda and Wydoski 1980; Miller et al. 1982; Tyus et al. 1982a, 1987; Haynes et al. 1984) have provided more quantitative approaches to the evaluation of fish habitat use and needs. In 1979, U.S. Fish and Wildlife Service (Service) developed standardized methods for studying the Colorado River fishes (Archer et al. 1980) and, in cooperation with the State of Colorado and the National Park Service, initiated fish studies in the Yampa River in fall 1980. The lower 198.4 km (Echo Park to near Williams Fork) was divided into eight relatively homogeneous river sections, using topographic and geologic maps, aerial surveys, and field reconnaissance, in an effort to evaluate habitat use of the rare fishes (Miller et al. 1982). The initial study area was extended to RK 224 because of angler-captured tag returns of Colorado squawfish from Craig, Colorado (see map opposite page 1). Data gaps identified in the initial studies (Miller et al. 1982) were evaluated in subsequent investigations using the same river stratification and fish sampling techniques.

Habitat use data were compiled for all fish species captured by U.S. Fish and Wildlife Service and Colorado Division of Wildlife biologists (e.g., major habitat type, depth, velocity, and substrate information) using radiotelemetry, electrofishing, trammel netting, angling, and seining. Reproductive behavior of Colorado squawfish in the Yampa River was studied from 1981 to 1988 (Wick et al. 1983; Archer and Tyus 1984; Tyus et al. 1987; present study). Studies of winter habitat use by Colorado squawfish and general habitat use by humpback chub were initiated in the Yampa River in 1986 (Karp and Tyus 1989; Wick and Hawkins 1989). Razorback sucker spawning and winter habitat use have also been investigated (Miller et al. 1982; Valdez and Masslich 1989; U.S. Fish and Wildlife Service, unpublished data). The present report includes data from published sources and unpublished data from Service files in Vernal, Utah.

In 1984, the Biology Subcommittee of the Upper Colorado River Basin Coordinating Committee and the U.S. Fish and Wildlife Service identified river reaches considered important to the survival and recovery of the rare Colorado River fishes (Upper Colorado River Basin Coordinating Committee 1984; Archer et al. 1986). This information was more recently updated in the Recovery Implementation Program (U.S. Fish and Wildlife Service 1987). We provide additional information for further delineation of critical river reaches in the Yampa River. This information is summarized in Fig. 4 and discussed in the following sections.

Colorado Squawfish

Adult

Adult Colorado squawfish are distributed in the mainstream Yampa River from its mouth upstream to Craig, Colorado (Fig. 4). The upper Yampa River (RK 81.6–198.4) is considered a concentration area for overwintering adults (Archer et al. 1986; Fig. 4), as evidenced by migration patterns of radio-tagged fish (Tyus et al. 1987) and abundance data (Miller et al. 1982;

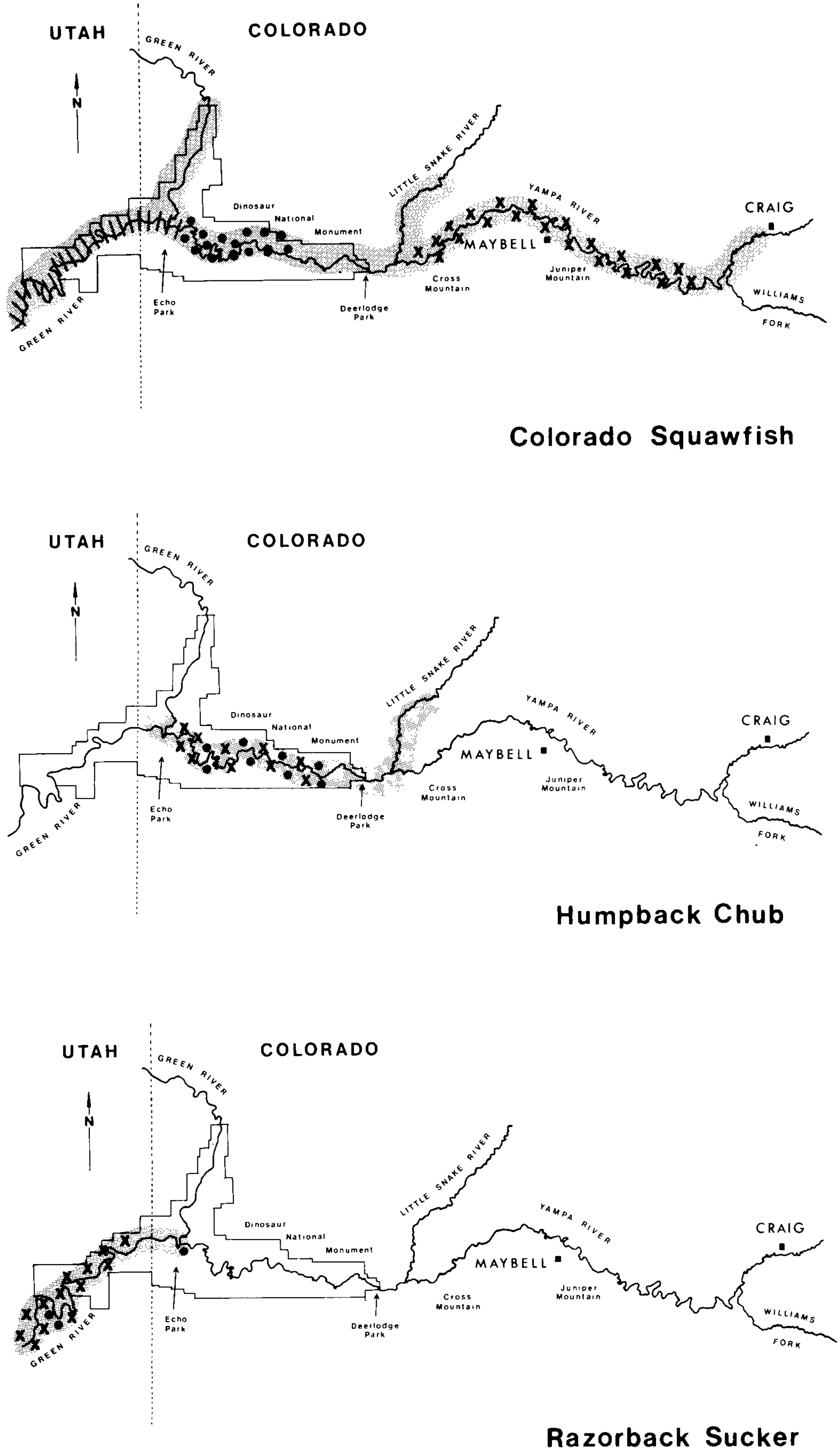

Fig. 4. Important river reaches for Colorado squawfish, humpback chub, and razorback sucker in Yampa and Green rivers, Colorado and Utah. *Shading* = distribution; *dots* = spawning areas; *X*'s = winter concentration, and //'s = larval drift.

Wick et al. 1985). During winter, adult Colorado squawfish use backwaters (ephemeral along-shore embayments), runs, and eddies, but are most common, and presumably feed, in shallow, ice-covered shoreline areas where large schools of minnows have been observed (Wick and Hawkins 1989). Local nonmigratory movements of adult Colorado squawfish in nonbreeding seasons may be indicative of home-range behavior (Tyus et al. 1987; Tyus 1989; Wick and Hawkins 1989).

In spring and early summer in the Yampa River, adult Colorado squawfish were most often located in backwater habitats or flooded bottomlands. Radio-tracking data indicated high use of shoreline backwater habitat in 1981 (a low-flow year; 66%, N = 6 individual fish) and high use of flooded bottomlands during 1983 (a high-flow year; 40%, N = 10). None of the 10 fish located during 1983 were in backwater habitat. Wick et al. (1983) noted that in 1982 (an average-flow year), adult Colorado squawfish used flooded shoreline areas in spring but moved to backwater habitats as the river level dropped. High use of flooded shorelines was also noted for adult Colorado squawfish in the Green River during the 2 high-flow years, 1983 and 1984 (Tyus et al. 1987).

Adult Colorado squawfish occupied a variety of habitats in mid-to-late summer, but were most common in eddies, pools, runs, and shoreline backwaters, over sand and silt substrates (Fig. 5). Visual observations in shallow water indicated that adults use sheltered microhabitats behind boulders, flooded vegetation, or other cover. During summer, radio-tagged fish were most often located in deeper shoreline habitats, where movements suggested heavy use of eddy-run interface (Tyus et al. 1987).

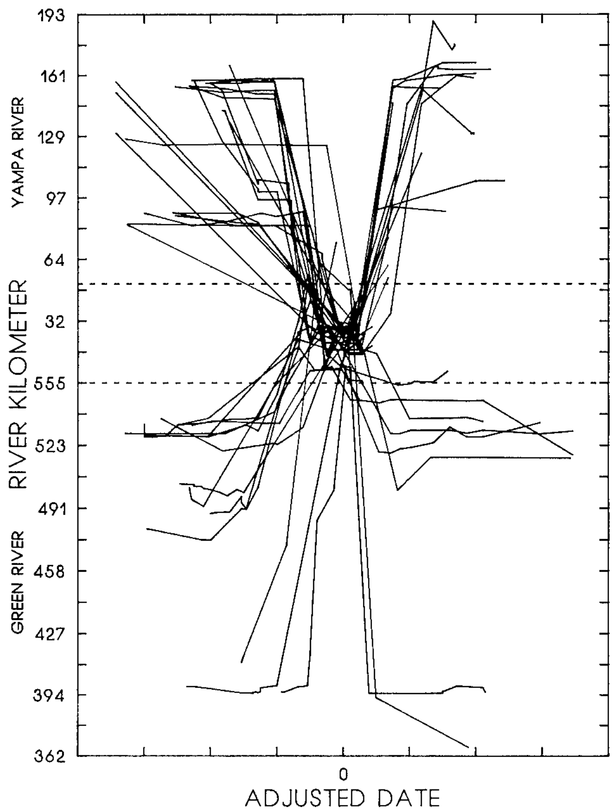

Fig. 6. Movement patterns of radio-tagged Colorado squawfish migrating to Yampa River spawning grounds, 1981–85, 1987, and 1988. Spawning reach is delineated by (===); 0 = midpoint of calculated optimum spawning period for each year. Adjusted date scale in 28-day increments.

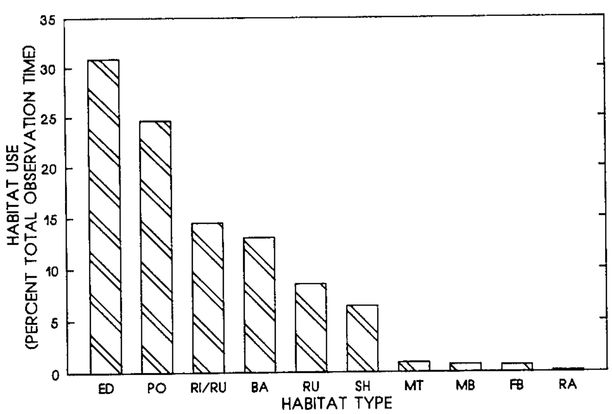

Fig. 5. Habitat use by radio-tagged Colorado squawfish in the Yampa River, June–August, 1981–85, 1987, 1988. ED = eddy; PO = pool; RI/RU = riffle/run <1.67 m depth; BA = backwater; RU = run >1.67 m depth; SH = shoreline; MT = mouth of tributary; MB = mouth of backwater; FB = flooded bottom; RA = rapid.

Spawning

Two major Colorado squawfish spawning migrations have been identified by Service biologists in the Green River basin by tracking radio-tagged fish. One migration was discovered in the Yampa River and upper Green River in 1981 (Tyus and McAda 1984), confirmed in 1982 (Wick et al. 1983), and again from 1983 to 1988 (Tyus et al. 1987). Movement patterns of fish migrating to the Yampa River spawning reach are presented for 1981–88 (Fig. 6). In May and early June, Colorado squawfish began downstream migrations in the Yampa and White rivers and upstream migrations in the Green River to spawn in riffle and pool habitat of the lower 51.2 km of the Yampa Canyon (Fig. 4). The only other confirmed Colorado squawfish spawning site in the Green River basin is in Gray Canyon (RK 224–256) of the Green River (Tyus et al. 1987; U.S. Fish and Wildlife Service, unpublished data).

A total of 43 Colorado squawfish were radio-tracked to the Yampa Canyon spawning reach by the U.S. Fish and Wildlife Service (N = 38) and Colorado Division of Wildlife (N = 5) from 1981 to 1988. These included 28 fish from the upper Yampa River, 13 fish from the Green River, and 2 fish from the White River. Average one-way movement of migrants radio-tracked by Service biologists was about 124.8 km. One of the White River fish migrated about 372.8 km to reach the Yampa River spawning grounds. This fish may have been en route for more than a year, because it was tagged at RK 164.8 of the White River in 1983, tracked to RK 49.6 of the Yampa River in spring 1984, and recaptured at RK 156.8 of the White River in 1985. These radio-tracking data show that migrating Colorado squawfish arrive in the Yampa Canyon in early summer from many areas throughout the upper Green River basin, including the White, Green, and upper Yampa rivers.

The initiation of the spawning migration is an important component of the reproductive cycle of the Colorado squawfish. To better evaluate some factors influencing the onset of migration, adult Colorado squawfish were radio-tracked in early spring in the upper Yampa River by U.S. Fish and Wildlife Service biologists in 1981 and 1983 (Tyus and McAda 1984; Tyus 1985), by Colorado Division of Wildlife and National Park Service personnel in 1982 (Wick et al. 1983), and by U.S. Fish and Wildlife Service and Colorado Division of Wildlife biologists in 1988. These fish initiated spawning migrations from 27 May to 13 June, depending on the type of water year (Table 1). Flows and water temperatures were highly variable within each migration period and among years. However, spawning migrations were initiated earlier in low-water years (e.g., 1981) and later in higher-water years (e.g., 1983; Table 1). Although radio-tracking studies were not conducted all years, data from 1981 (low-water year), 1982 and 1988 (average-water years), and 1983 (high-water year) were used to investigate relations between discharge, water temperature, and date of initiation of spawning migration (Figs. 7 and 8). As shown in Fig. 8, spawning migrations of radio-tagged Colorado squawfish (N=24) were associated with highest spring flows and river temperatures generally exceeding 14°C. However, the actual period of initiation of spawning migration of Colorado squawfish may be longer because radio-tagged fish may not have included early and late migrants.

Timing of the reproductive cycle is influenced first by intrinsic biological mechanisms and secondly by environmental stimuli (Brown et al. 1970). Identification of these stimuli is made difficult by synergistic and other confounding interrelations (Bye 1984). We believe that some complex combination of endogenous (e.g., stage of maturity, physiological condition, genetic lineage) and exogenous factors (e.g., substrate, temperature, discharge, photoperiod) are necessary and that neither discharge nor temperature alone is sufficient to induce spawning migrations or spawning. For example, radio-tracking data suggest that all adult Colorado squawfish do not spawn each year. Of four fish radio-tracked to spawning grounds at least once in consecutive years (1+ years) during the spawning season, two migrated only 1 year and presumably did not spawn each year.

Effects of exogenous factors on reproductive cycles of cyprinid fishes are well known and many physicochemical variables have been implicated (reviewed by Brown et al. 1970; Bye 1984; McKeown 1984). We hypothesize that inputs of certain chemical substances from runoff and inundated shorelines during spring snowmelt, in concert with increasing river level and temperatures, may act to influence genetic, physiological, and behavioral mechanisms in Colorado squawfish that are associated with spawning migrations. We assume these mechanisms can only be activated at

Table 1. *Initiation of Colorado squawfish spawning migrations, Yampa River spawning grounds, 1981–83, 1988. Movement recorded for 24 radio-tagged fish (1981 = 7 fish, 1982 = 5 fish, 1983 = 7 fish, 1988 = 5 fish). Data for 1982 after Wick et al. (1983).*

Year	Type water year[a]	Initiation of migration[b]	Discharge[c] (m^3/s) Mean	Discharge[c] (m^3/s) Range	Water temperature (°C)[c] Mean	Water temperature (°C)[c] Range
1981	Low	27 May–20 June	121.1	33.6–171.8	14.9	12.5–18.5
1982	Average	10 June–3 July	200.7	175.5–235.2	13.7	11.6–15.7
1983	High	13 June–12 July	240.7	127.4–322.6	13.8	9.2–17.3
1988	Average	9–23 June	129.8	93.4–193.1	15.8	13.8–19.4

[a] Designation of low, average, and high water years based on average annual discharge for 1922–87: low, <43.15 m^3/s; average, 43.15–77.83 m^3/s; high, >77.83 m^3/s (M. Butler, personal communication).

[b] Initiation of migration is the period between first and last departure of radio-tagged fish in upper Yampa River to Yampa Canyon spawning grounds.

[c] Data based on daily averages during indicated period (USGS flow records, Yampa River near Maybell, Colorado).

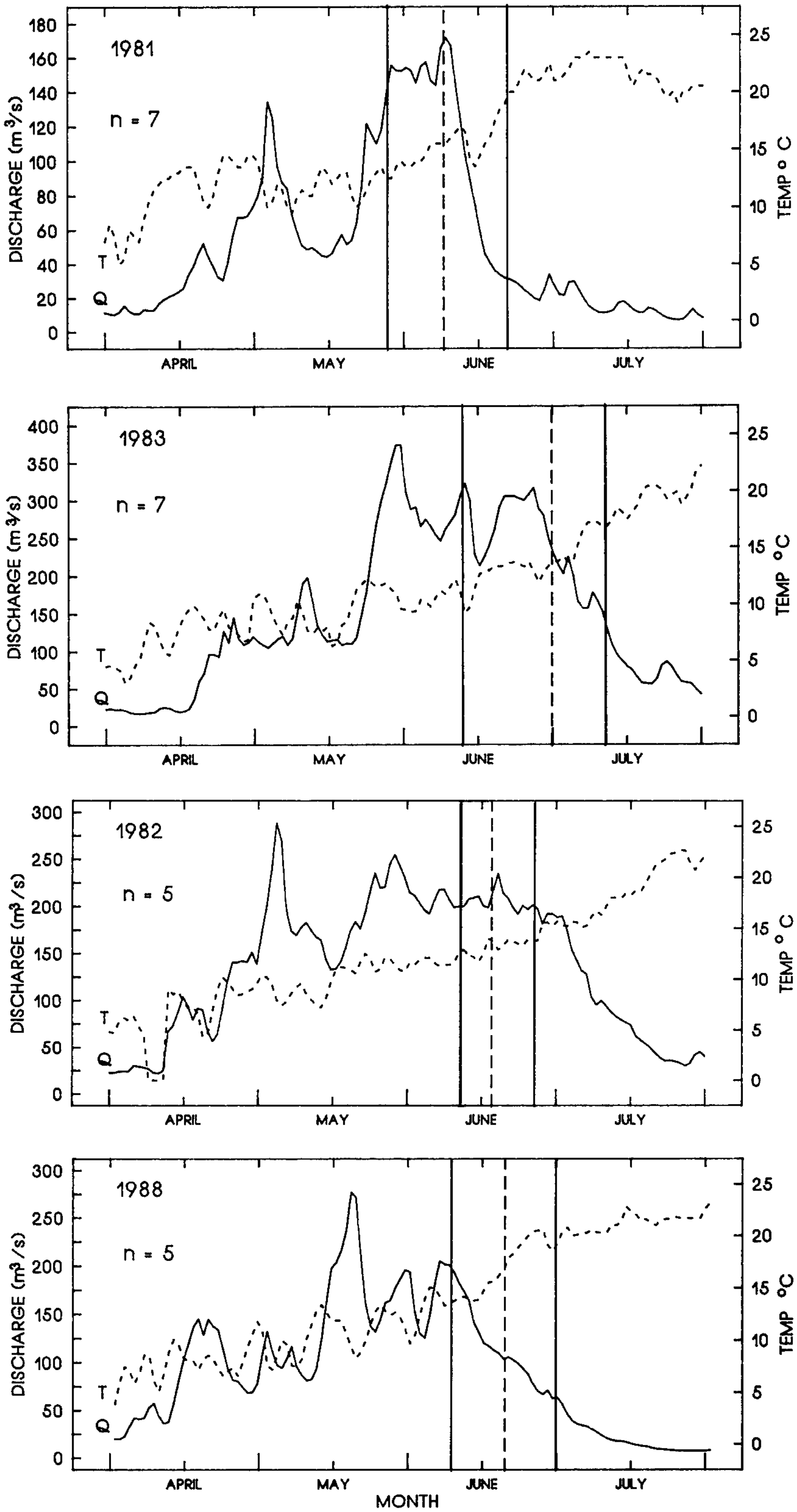

Fig. 7. Relation between discharge, temperature, and initiation of spawning migration for Colorado squawfish, Yampa River, 1981–83 and 1988. Q = average daily discharge; T = average daily temperature (USGS records, Yampa River near Maybell, Colorado). *Solid vertical lines* = dates first and last radio-tagged fish exhibited movement to spawning ground; *dashed vertical line* = average date radio-tagged fish exhibited migratory movements; *n* = number of radio-tagged fish.

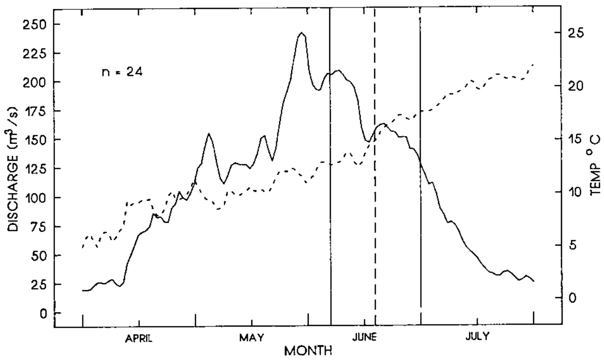

Fig. 8. Relation between average discharge, temperature, and initiation of spawning migration for Colorado squawfish, Yampa River, 1981–83 and 1988 combined. *Solid vertical lines* = average dates first and last radio-tagged fish exhibited movement to spawning ground; *dashed vertical line* = average date all radio-tagged fish exhibited migratory movements; *n* = number of radio-tagged fish.

certain times due to intrinsic biological rhythms, as discussed by McKeown (1984).

Homing behavior in Colorado squawfish is indicated by long-distance movement patterns and repeated recaptures of the same fish on the Yampa River spawning grounds in subsequent years (Wick et al. 1983; Tyus 1985). Of four fish radio-tracked to the Yampa River spawning reach for more than 1 year, two migrated to the same location in consecutive years, indicating a fidelity to this spawning site. Recaptures of fish on the Yampa River spawning grounds also support the concept of fidelity in Colorado squawfish. Five Colorado squawfish in breeding condition were tagged and recaptured in the Yampa River between RK 17.6 and 28.8 for intervals of 1+ years (three fish for 2 consecutive years, one fish after a 2-year interval, and one fish after a 3-year interval). Adult Colorado squawfish using the Yampa River spawning grounds have not been found to use any other spawning site in the Green River system. This suggests that these spawning areas are unique and critical to the conservation of the species.

The Groundwater Seepage Hypothesis, proposed for other species by Harden-Jones (1981), may be implicated as a possible homing mechanism for Colorado squawfish (Tyus 1985). Migrating adult Colorado squawfish pass through miles of potentially good spawning habitat (i.e., canyon-bound cobble bars in Split and Whirlpool canyons in the Green River for downstream fish; upper Yampa Canyon, Cross Mountain Canyon, and Juniper Mountain Canyon in the upper Yampa River for upstream fish) to reach specific spawning grounds in the Yampa Canyon. Although no experimental evidence to date confirms or disproves the existence of an olfactory imprinting mechanism for Colorado squawfish, observations at the two confirmed spawning grounds in upper Green River basin indicated that Colorado squawfish that migrate to these areas may be orienting to them because of freshwater inflow from spring-fed tributaries (e.g., Florence Creek, Green River; Warm Springs Creek, Yampa River) and sandstone-limestone seeps (e.g., at Coal Creek, Green River; at Cleopatra's Couch, Yampa River).

There is good agreement between the arrival of migrating fish on spawning grounds, collections of ripe fish, and estimated dates of egg deposition (Fig. 9). These data were used to estimate total and optimal spawning periods (Table 2). Total spawning period included widest range of activities associated with

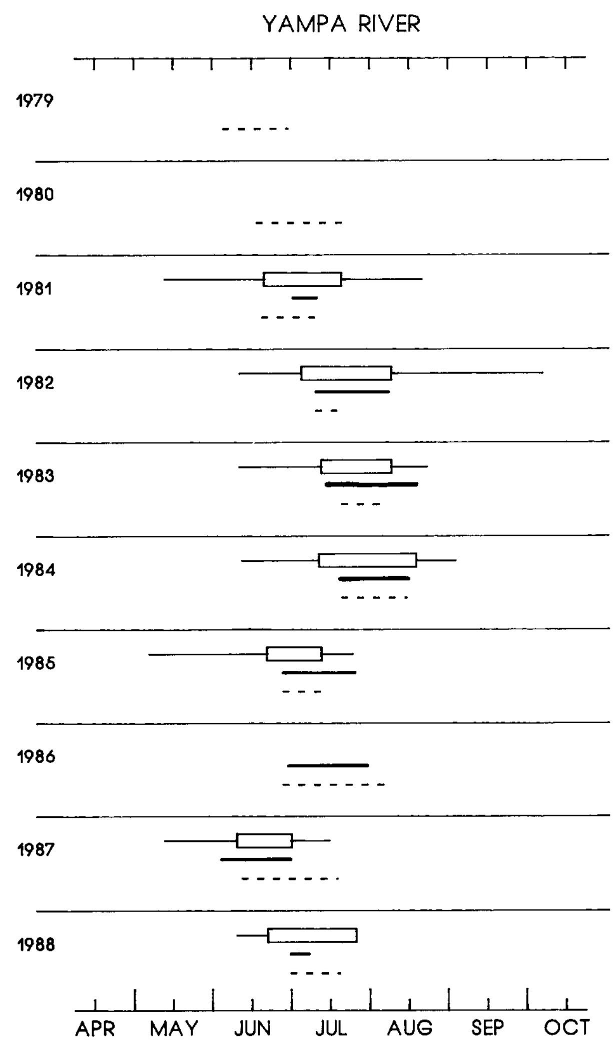

Fig. 9. Migration of radio-tagged Colorado squawfish (—); collections of ripe Colorado squawfish (▬); and dates of estimated egg deposition (- -), Yampa River, 1981–88. □ indicates presence of radio-tagged fish on spawning grounds.

Table 2. *Dates of egg deposition, collections of ripe fish, presence of radio-tagged fish on spawning grounds, and spawning period, Colorado squawfish, Yampa River, 1981–88.*

Year	Egg deposition[a]	Ripe fish	Radio-tagged fish[b]	Spawning period[c] Total	Spawning period[c] Optimum
1981	19 June–10 July	1–10 July	20 June–20 July	19 June–20 July	23 June–13 July
1982	10–18 July	10 July–7 August	4 July–8 August[d]	4 July–8 August	8 July–1 August
1983	20 July–5 August	14 July–18 August	12 July–8 August	12 July–18 August	15 July–10 August
1984	19 July–13 August	18 July–14 August	10 July–17 August	10 July–17 August	16 July–15 August
1985	27 June–13 July	27 June–25 July	21 June–12 July	21 June–25 July	25 June–17 July
1986	27 June–5 August	5–30 July	N/A	27 June–5 August	1 July–2 August
1987	11 June–16 July	3–30 June	9–30 June	3 June–16 July	8 June–5 July
1988	27 June–19 July	29 June–6 July	20 June–24 July	20 June–24 July	25 June–16 July

[a] Dates obtained from back-calculations of larval age using equations in Nesler et al. (1988).
[b] Dates represent first and last appearance of radio-tagged fish on spawning grounds.
[c] Total includes all indication of spawning activity; optimum is the average of dates for egg deposition, collections of ripe fish, and presence of migrating radio-tagged fish on spawning grounds.
[d] Data provided by Wick et al. (1982).

spawning (e.g., presence of migrating radio-tagged fish on spawning grounds, collections of ripe fish, or calculated dates of larval emergence in spawning reach) and lasted 4–5 weeks. Optimum spawning period was the time of greatest spawning activity, calculated by averaging the dates when radio-tagged fish and ripe fish were present in the spawning reach and back-calculated dates of egg deposition.

From 1981 to 1988, spawning requirements of Colorado squawfish were evaluated in the Yampa River spawning reach. The length of the estimated optimal spawning period – about 26 days – was similar for all years (Table 3). Spawning generally occurred earlier in lower-water years – 1981, 1987, and 1988 – and later in high-flow years – 1983 and 1984 (Table 3). Water temperature and discharge varied between years during the optimum spawning period (Table 3). Water temperatures ranged from 14.5°C to 27.5°C for all years. Average minimum temperature was 19°C and average maximum temperature was 24°C. During optimum spawning period, mean discharge ranged from 25.27 m^3/s (1981) to 108.25 m^3/s (1982).

Vanicek and Kramer (1969) first suggested that discharge and temperature influenced spawning in

Table 3. *River conditions during optimum spawning period, Colorado squawfish, Yampa River, 1981–88.*

Year	Water year[a]	Period of optimum spawn[b]	Discharge[c] Mean	Discharge[c] Range	Water temperature (°C)[d] Minimum (mean)	Water temperature (°C)[d] Maximum (mean)	Water temperature (°C)[d] Range
1981	Low	23 June–13 July	25.27	12.37–37.55	19.3	24.8	18.0–25.5
1982	Average	8 July–1 August	108.25	68.77–176.31	19.5	23.3	16.5–27.5
1983	High	15 July–10 August	86.17	41.6–141.22	21.0	24.3	18.0–27.0
1984	High	16 July–15 August	71.74	29.43–131.60	20.3	23.8	20.0–24.0
1985	High	25 June–17 July	64.02	28.58–135.84	17.8	22.8	14.5–25.5
1986	High	1 July–2 August	69.82	26.41–145.46	19.5	22.5	18.5–23.0
1987	Low	8 June–5 July	58.69	23.97–128.20	17.9	22.5	16.5–24.5
1988	Average	25 June–16 July	49.14	15.73–104.43	19.5	23.0	18.0–25.0

[a] Designation of low-, average-, and high-water years based on average annual discharge for 1922–87: low, <43.15 m^3/s; average, 43.15–77.83 m^3/s; high, >77.83 m^3/s (M. Butler, personal communication).
[b] Derived from back calculations of larval age, and contact with radio-tagged adults and collection of ripe fish on spawning ground.
[c] USGS flow records (1981 sum of Yampa River near Maybell, Colorado, and Little Snake River near Lily, Colorado; 1982–88 Yampa River at Deerlodge Park, Colorado). Data are daily discharges for optimum spawning period.
[d] USGS flow records (1981 Yampa River near Maybell, Colorado, 1982 Yampa River at Deerlodge Park, Colorado) and hand-held thermometers (1983–88, minimum (mean) and maximum (mean) values were calculated from early morning and afternoon temperatures taken on the spawning grounds because a continuous temperature recorder was not present).

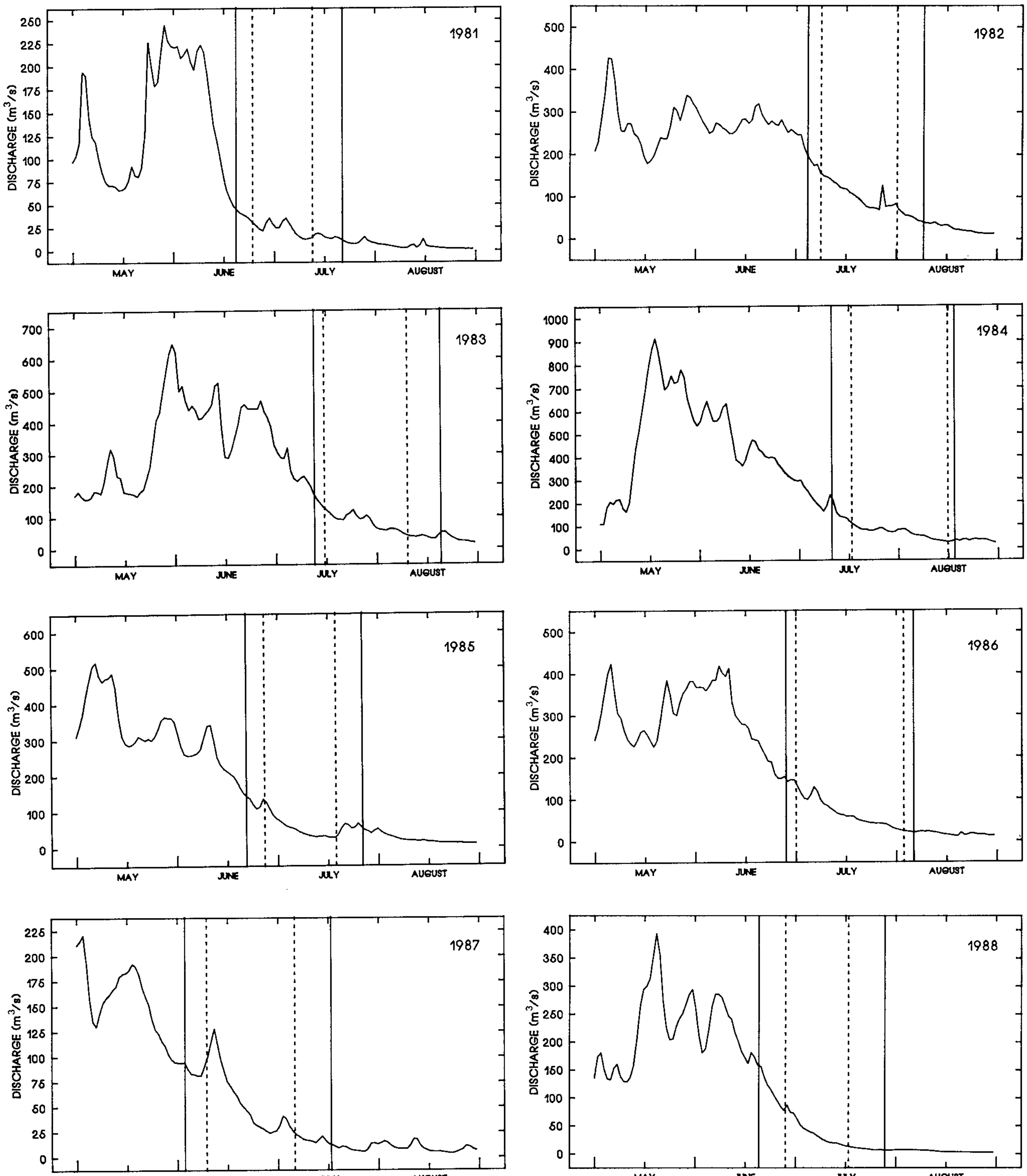

Fig. 10. Relation between discharge and spawning period for Colorado squawfish, Yampa River, 1981–88. *Solid vertical lines* = total spawning period; *dashed vertical lines* = optimum spawning period (USGS records: 1981—Yampa River near Maybell, Colorado, and Little Snake River near Lily, Colorado; 1982–88—Yampa River at Deerlodge, Colorado).

Colorado squawfish. Service data from 1981 to 1988 indicated that spawning occurs with declining flows (following spring runoff) and increasing temperatures (Fig. 10) – about 26 days (range: 17–33 days) after migration. Regression analyses and multiple regression techniques were used to investigate possible cause-effect relations between spawning period, discharge, and temperature for 1981–88. Peak discharge preceding spawn, and mean minimum temperatures during spawn, were highly correlated with the spawning period ($r = 0.84$ and $r = 0.88$, respectively; $P < 0.05$), ostensibly because discharge, temperature, and spawning period are correlates. We do not presume the above relations represent all conditions necessary for successful spawn – rather, spawning of Colorado squawfish is a result of complex environmental and biological influences and is not triggered by a single flow or temperature event. For example, Nesler et al. (1988) hypothesized that flow spikes from rainstorms during spring runoff may be important influences on ovulation and spawning in Colorado squawfish.

Colorado squawfish spawn in the lower 51.2 km of the Yampa River, particularly in a reach extending from Warm Springs Rapid (RK 6.56) to the vicinity of Harding Hole (RK 32; Tyus et al. 1982b, 1987; Wick et al. 1983; Haynes et al. 1984; McAda and Tyus 1984). Numerous captures of ripe fish in a 6.4 km reach near Mathers Hole (RK 28.3) suggest that egg deposition and fertilization may be concentrated in this area (Fig. 4), where large, deep pools and eddies are intermingled with runs and cobble bars of gravel, cobble, and boulder substrates.

Spawning behavior of Colorado squawfish was divided into two phases: (1) a resting-staging phase in pools or large shoreline eddies, where the fish may find suitable resting and feeding habitat between spawning forays or where males aggregate until females are ripe; and (2) a deposition-fertilization phase on cobble bars, where actual spawning occurs (Archer and Tyus 1984). Breeding adults occupied pools or eddies having an average depth and velocity of 2 m and 0.2 m/s, respectively, and cobble bars with an average depth and velocity of 1 m and 0.5 m/s (Table 4).

Breeding adults were most often concentrated in river reaches containing deep pools, eddies, and cobble (rubble) bars. Radio-tagged fish moved from pools or eddies to cobble-gravel bars (where they presumably spawned). This behavior is similar to that of spawning northern squawfish (Beamesderfer and Congleton 1981). Turbid conditions in the Yampa River have precluded direct observations of egg deposition; however, cobbles removed from the substrate during that time of year are clean of sediment and algae

Table 4. *Depths and velocities taken at location of radio-tagged Colorado squawfish on Yampa River spawning grounds, 1981, 1983, 1984, 1985, 1987, and 1988.*

Year[a]	Number of fish	Number of contacts[b]	Depth (m) Mean	Depth (m) Range	Velocity (m/s) Mean	Velocity (m/s) Range
			Resting-Staging[c]			
1981	7	74	1.80	(0.76–2.68)	0.39	(0.03–1.19)
1983	7	46	2.36	(1.07–5.79)	0.47	(0.09–1.46)
1984	5	261	1.70	(0.76–3.05)	0.17	(0.00–0.40)
1985	3	77	3.30	(0.76–4.27)	0.22	(0.00–0.30)
1987	4	22	1.97	(1.28–2.74)	0.14	(0.06–0.18)
1988	2	8	2.86	(2.74–3.05)	0.06	(0.06)
Weighted Mean			2.06		0.24	
			Deposition-Fertilization[d]			
1981	7	65	1.16	(0.61–1.68)	0.59	(0.36–1.20)
1983	4	21	1.02	(0.55–1.22)	0.79	(0.27–1.04)
1984	6	82	0.89	(0.61–1.52)	0.40	(0.09–1.01)
1985	1	1	1.52	—	0.15	—
1988	3	12	0.87	(0.46–1.22)	0.48	(0.15–0.92)
Weighted Mean			1.01		0.52	

[a] No fish located in deposition-fertilization habitat in 1987.
[b] One contact = one 15-min period of observation.
[c] Includes eddy and pool habitat.
[d] Includes riffle and shallow run habitat over cobble and boulder substrate.

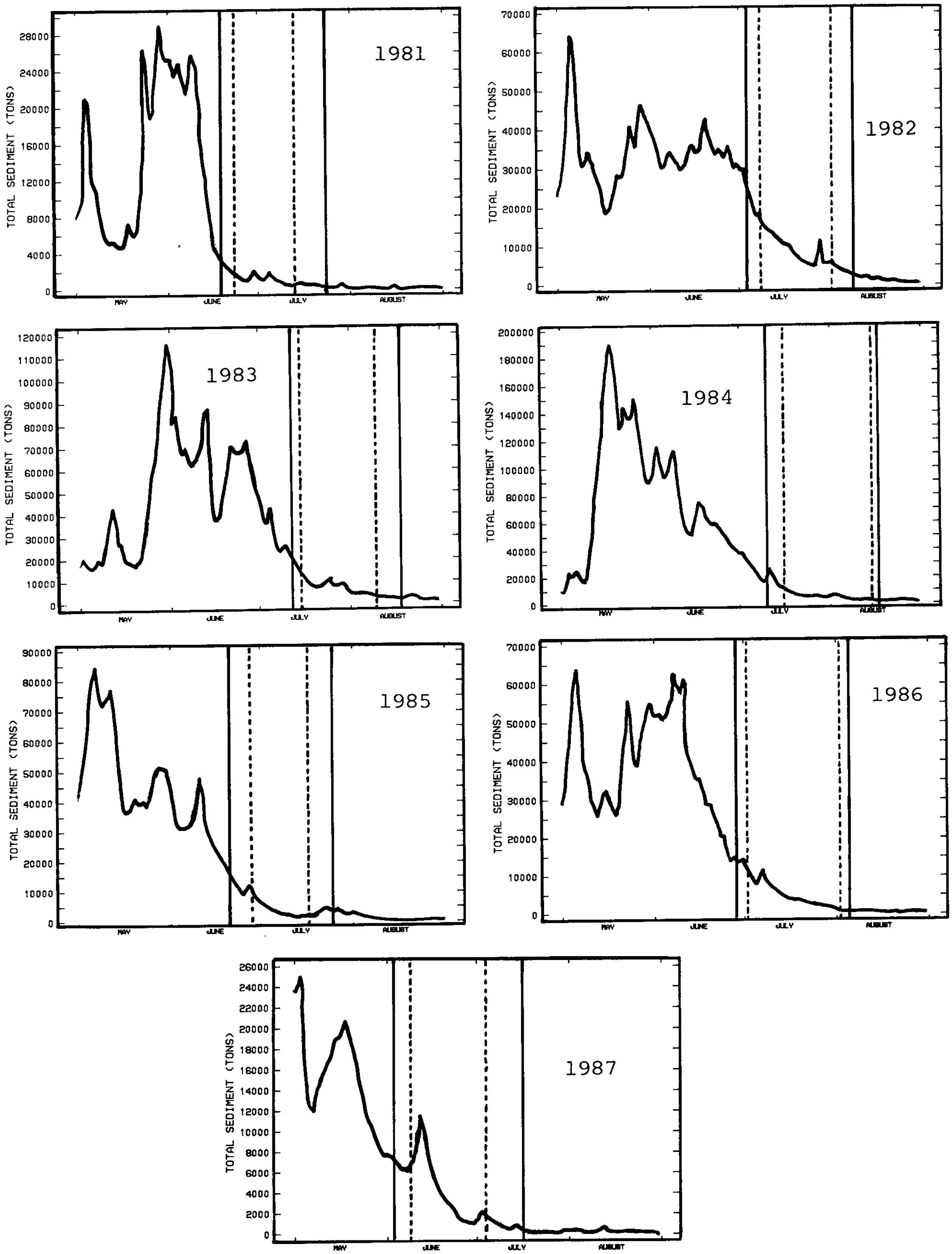

Fig. 11. Relation between total sediment discharge and spawning period for Colorado squawfish at Mathers Hole (river kilometer 26.4), Yampa River, 1981–87 (courtesy M. Butler). *Solid vertical lines* = total spawning period; *dashed vertical lines* = optimum spawning period.

(Archer and Tyus 1984; U.S. Fish and Wildlife Service, unpublished data). There is substantial field and laboratory data showing that Colorado squawfish and other squawfish species require cleaned cobble surfaces for successful egg adhesion (Burns 1966; Patten and Rodman 1969; Hamman 1981). Hamman (1981) noted hatching of Colorado squawfish larvae from cobble surfaces. The need for cleaned cobble and boulder substrates is supported by the repeated spawning of Colorado squawfish following peak flows and peak sediment transport (Figs. 10 and 11).

Three hundred eight Colorado squawfish (including 208 ripe adults) were collected by Service biologists at the two confirmed spawning sites in the Yampa and Green rivers during spawning periods from 1981 to 1988 (Table 5). The fish were classified ripe if milt or eggs could be expressed from the vent with light hand pressure on the abdomen. Ripe males (N = 194) were bronze colored and heavily covered with breeding tubercles. Twenty-five additional fish were classified as suspected males because of the presence of these two characteristics, even though milt could not be expressed. Robust tuberculation in ripe male Colorado squawfish was also noted by Seethaler (1978) and Hamman (1981). Only 14 ripe or spent female Colorado squawfish were positively identified based on the expression of eggs. However, 42 additional fish were classified as suspected females because of their large size and the absence of heavy tuberculation and bronze coloration. These data indicate a paucity of adult female Colorado squawfish in the Green River system, which may be due to differential mortality (Tyus et al. 1987). A high male to female ratio was previously noted for both Colorado squawfish (Seethaler 1978) and other squawfish species (Patten and Rodman 1969).

Larvae and Postlarvae

Larval Colorado squawfish emerge as sac fry from cobble bars in the Yampa Canyon and drift downstream (Tyus et al. 1982b; Haynes et al. 1984; Fig. 4) to concentrate in shallow backwater habitats in the Green River (Tyus et al. 1982b, 1987; Fig. 12). About 16 days are required for transport of newly emerged Colorado squawfish fry to the mouth of the Yampa River from the midpoint of the spawning grounds (RK 26.4–29.1; U.S. Fish and Wildlife Service, unpublished data). From 1979 to 1981, peaks of abundance of young Colorado squawfish were noted to occur about 160 km downstream of the Yampa River spawning reach (Tyus et al. 1982b). Presumably, young fish use river current

Table 5. *Spawning collections of Colorado squawfish, Yampa and Green rivers, from June to August, 1981–88.*

			Males				Females			
			Ripe		Suspected[d]		Ripe		Suspected[e]	
Year	River	N[a]	n[b]	TL[c]	n	TL	n	TL	n	TL
1981	Yampa	35	20	538	6	528	1	779	2	748
1981	Green	4	1	478	0	—	0	—	0	—
1982	Yampa	1	1	547	0	—	0	—	0	—
1982	Green	11	6	509	0	—	0	—	2	642
1983	Yampa	22	13	596	1	560	3	722	2	662
1983	Green	14	11	569	0	—	0	—	1	625
1984	Yampa	38	20	560	1	510	3	666	11	714
1984	Green	29	14	574	4	544	1	750	6	671
1985	Yampa	13	10	571	0	—	1	723	1	639
1985	Green	36	24	574	5	549	0	—	2	626
1986	Yampa	12	7	535	0	—	1	485	3	702
1986	Green	24	22	541	1	559	0	—	1	781
1987	Yampa	19	13	539	1	510	0	—	4	621
1987	Green	25	16	533	4	520	0	—	4	666
1988	Yampa	5	4	544	0	—	0	—	1	725
1988	Green	20	12	563	2	588	4	565	2	684
Total	Yampa	145	88	555	9	528	9	683	24	693
Total	Green	163	106	555	16	546	5	602	18	667

[a] N = all fish captured on spawning grounds.
[b] n = ripe or suspected male and female.
[c] TL = average total length in millimeter.
[d] Heavily tuberculated and bronze-colored fish, but with no expressible sex products.
[e] Large fish with little bronze coloration, little or no tuberculation, and large vent.

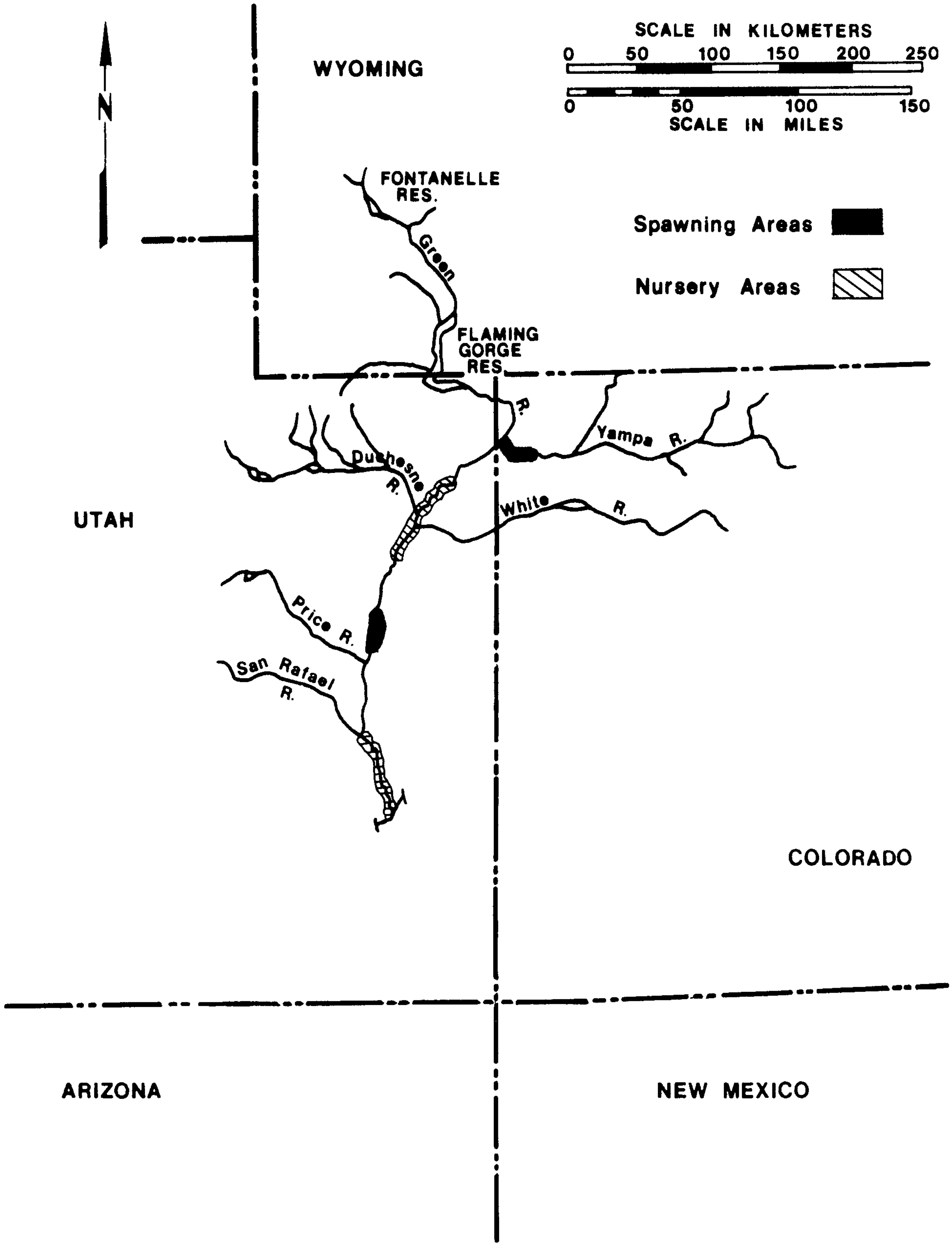

Fig. 12. Colorado squawfish spawning and primary nursery habitat in the Green River basin, Colorado and Utah.

for dispersal from upstream spawning grounds to downstream nursery habitats (Tyus and McAda 1984; Tyus 1986; Paulin et al., in review). These productive nursery habitats are created during summer by gradually decreasing flows following spring runoff. Postlarval (young-of-the-year) Colorado squawfish are rare in the Yampa River, the farthest upstream record of postlarval Colorado squawfish in the Yampa River is RK 24 (Haynes et al. 1984).

Juvenile

Distribution, abundance, and habitat use of juvenile Colorado squawfish (60–450 mm total length) in the Yampa River are poorly understood because of the rarity of this life history stage (Miller et al. 1982; Wick et al. 1983, 1985). From 1980 to 1988, only 3% (N = 198) of all Colorado squawfish greater than 60 mm collected by Service biologists in the Yampa River were juveniles.

The downstream drift of larvae from Yampa River spawning grounds suggests that a long-distance upstream movement by juveniles is needed to repopulate upstream areas (Tyus 1986). Such movement probably occurs during the late juvenile or early adult stage, because only large-sized fish are found in the upper Yampa River. This phenomenon is also supported by data from the Green River showing large concentrations of larger juvenile Colorado squawfish (average electrofishing catch, >0.18 fish per hour) in the lower section of the mainstream Green River and greatest concentrations of adults (average electrofishing catch, >0.6 fish per hour) in upstream sections (Tyus et al. 1987).

Humpback Chub

Adult

Adult humpback chubs (>230 mm) were captured in canyon-bound habitat in the lower 89.6 km of the Yampa River (Tyus et al. 1982a; Karp and Tyus 1989; C. Haynes, personal communication) and in the lower 16 km of the Little Snake River (E. Wick, personal communication; Fig. 4). Service biologists captured seven adult humpback chubs in the Yampa River (RK 28.8–75.2) from 1981 to 1985. From 1986 to 1988, expanded efforts between RK 6.4 and 73.6 yielded 88 captures (9 recaptures). Adult humpback chubs were most often collected in eddy habitat (average depth, 2 m), particularly in shoreline eddies created by large boulders and rapids (Karp and Tyus 1989). Adult humpback chub were commonly captured with roundtail chub and the introduced channel catfish (*Ictalurus punctatus*; Karp and Tyus 1989). Classification of the adult life history stage was based on the smallest ripe humpback chub captured, a 232-mm male in Whirlpool Canyon, Green River.

Spawning

Spawning of the humpback chub in Yampa Canyon was documented in 1986 with the capture of two spent females and two ripe males (Tyus et al. 1987). This was confirmed in 1987 with the capture of 2 ripe females, 7 ripe males, and 11 tuberculated fish (sex not determined, 2 recaptures); and in 1988 with the capture of 1 ripe female, 5 ripe males, and 2 tuberculated fish (1 1987 recapture; Karp and Tyus 1989). Thus, a total of 32 mature humpback chubs (3 recaptures) were captured in spawning condition in Yampa Canyon, RK 19.2–64, in shoreline eddy and run habitat (Fig. 4). Humpback chubs spawn shortly after peak spring flows (Fig. 13; 1986 not included because sampling was initiated following highest spring flows). This relation has also been noted in the Blackrocks area of the upper Colorado River (Valdez and Clemmer 1982; Archer et al. 1985) and in the Little Colorado River, Arizona (Kaeding and Zimmerman 1983; C. O. Minckley, personal communication).

Although specific discrimination of Colorado River *Gila* is problematical in some areas (Holden and Stalnaker 1970; Valdez and Clemmer 1982), chubs captured in the Yampa River in 1987 and 1988 were

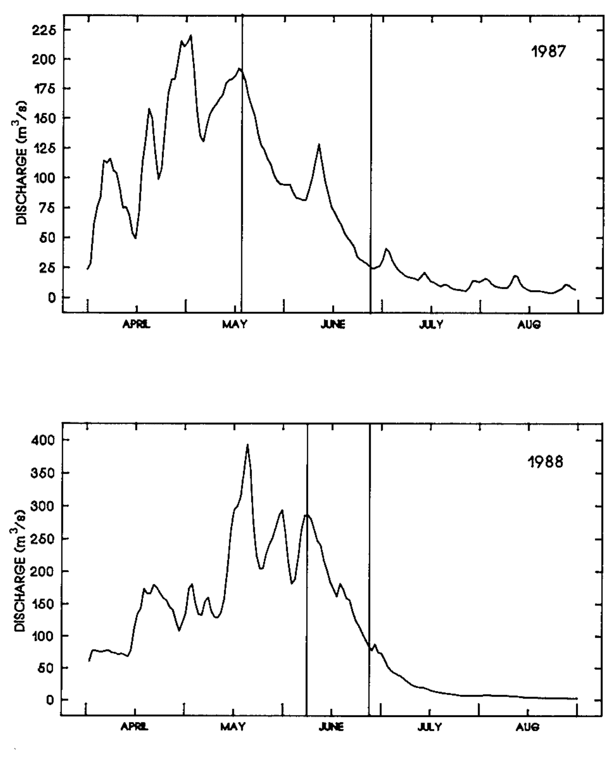

Fig. 13. Relation between discharge and spawning period for humpback chub, Yampa River, 1987–88. *Vertical bars* delineate spawning period.

distinguished as either the humpback form or the roundtail form, following a qualitative and quantitative inspection (Douglas et al. 1989; Karp and Tyus 1989). This suggests that the morphological variation apparent in some locations where *Gila* intermediates occur (reviewed by Valdez and Clemmer 1982) may be induced by recent habitat change. Thus, the presence of intermediate forms in altered systems (e.g., Green River and Colorado River) and the apparent absence of such forms in unaltered rivers (e.g., Yampa River and Little Colorado River) emphasizes the importance of natural riverine environments for recovery of the humpback chub.

Juvenile, Post Larvae, Larvae

Thirteen juvenile (168 mm–227 mm) humpback chubs have been collected between RK 0.16 and 64 in the Yampa Canyon by U.S. Fish and Wildlife Service biologists (Karp and Tyus 1989). Classification of juvenile *Gila* as the humpback form was based on the same complex of morphologic characters used to differentiate the adult life history stage (Karp and Tyus 1989). Most young humpback chubs were captured in shoreline eddies and runs. Problems with specific identification of small *Gila* in the upper Colorado River basin have hindered the evaluation of habitat needs of small humpback chubs. However, young-of-the-year humpback chubs have been tentatively identified in the lower 64 km of the Yampa Canyon (R. T. Muth and D. E. Snyder, personal communication).

Bonytail Chub

Habitat requirements of the bonytail chub in the Green River basin are largely unknown. Fish collections in Echo Park (DNM) before and after closure of Flaming Gorge Dam indicated that the species was present in fair numbers at the confluence of the Yampa and Green rivers (Vanicek 1967). However, recent investigations in that area have yielded few captures. Holden and Stalnaker (1975) reported the capture of 36 bonytail chubs in the Yampa (lower 16 km) and upper Green rivers between 1968 and 1970. Holden and Crist (1981) collected one bonytail chub in the lower Yampa River in 1979, and Service biologists captured one suspected juvenile in 1987. Additional habitat use information is expected from a radio-tracking study of adult bonytail chubs introduced into the upper Green River (DNM) in 1988 and 1989 (T. Chart, personal communication).

Razorback Sucker

Adult

More than 500 adult razorback suckers have been captured in flat-water sections of the upper Green River (RK 282–552) and in the lower 21 km of the Yampa River (Azevedo 1962; Vanicek et al. 1970; Holden and Stalnaker 1975; Seethaler et al. 1979; McAda and Wydoski 1980; Miller et al. 1982; Tyus et al. 1982b; Tyus 1987; U.S. Fish and Wildlife Service, unpublished data; Fig. 5). During the nonbreeding season, adult razorback suckers were most common in shoreline runs and mid-channel sand bars in the mainstream Green River, with an average water depth of <2 m and an average velocity of <0.5 m/s (Tyus 1987). Adult razorback suckers overwinter in the Echo Park area of DNM (McAda and Wydoski 1980; Valdez and Masslich 1989).

Spawning

Spawning activity of the razorback sucker has been documented in the lower Yampa River near its confluence with the Green River and in the upper Green River (McAda and Wydoski 1980; Miller et al. 1982; Tyus 1987; U.S. Fish and Wildlife Service, unpublished data; Fig. 5). Thirty-two ripe razorback suckers (6 females, 26 males; including 2 recaptures) were captured on cobble and gravel bars in the lower Yampa River in 1975, 1981, 1988, and 1989 at an average depth of 0.61 m and an average velocity of 0.64 m/s (McAda and Wydoski 1980; Miller et al. 1982; U.S. Fish and Wildlife Service, unpublished data). During this period, water temperatures were variable but averaged 15°C. The recapture of a ripe male razorback sucker in the lower Yampa River (RK 0.16) in 1988 that had originally been captured in the same locality in 1981 (also ripe), indicates a fidelity to this spawning site. This fish moved at least 52.8 km in 1988 from the upper Green River to reach the lower Yampa River to spawn.

Spawning of razorback suckers occurred on the ascending limb of the spring hydrograph (Fig. 14; spawning period in 1988 delineated by a single bar because ripe fish were collected only one day). This pattern of razorback suckers spawning during spring runoff was also noted in the upper Green River (Tyus 1987; U.S. Fish and Wildlife Service, unpublished data).

The capture of ripe razorback suckers in the lower Yampa and upper Green rivers and the tentative identification of larvae in upper Green River seine collections (R. T. Muth and D. E. Snyder, personal communication) indicates that razorback suckers reproduce successfully in the upper Green River basin (McAda and Wydoski 1980; Tyus 1987; U.S. Fish and Wildlife Service, unpublished data). However, there is little indication of widespread recruitment to the juvenile stage throughout the Colorado River basin (Holden 1978; McAda and Wydoski 1980; Minckley 1983; Tyus 1987; Marsh and Minckley 1989). Habitat requirements of this species in riverine environments are not well known because of the scarcity of extant populations (Minckley 1983; Lanigan and Tyus 1989)

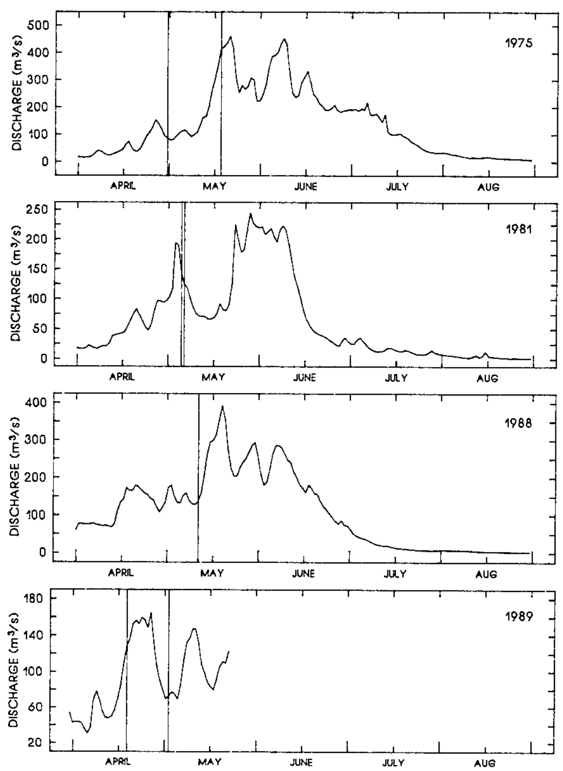

Fig. 14. Relation between discharge and spawning period for razorback sucker, Yampa River, 1975, 1981, 1988, and 1989 (discharge data incomplete for 1989). *Vertical bars* delineate spawning period. (One collection of ripe fish in 1988.)

and the absence of juvenile and subadult life history stages (McCarthy and Minckley 1987; Tyus 1987). The apparent decline of the razorback sucker toward extinction throughout the Colorado River basin emphasizes the need for more immediate measures toward recovery of this species.

Limiting Factors

An evaluation of limiting factors is difficult because of complex relations between environmental and biological variables that limit the distribution and abundance of organisms. A limiting factor is simply one component of a multidimensional system. Thus, single factor studies (e.g., determination of temperature threshold for successful reproduction) should be evaluated from a holistic perspective for application in natural systems and not in isolation. We stress the need for system-level cognizance and interpretation in evaluating factors that are potentially limiting to species in decline.

Studies of factors limiting the distribution and abundance of rare fishes in the Yampa River are complicated by the variability of the environment (e.g., seasonal fluctuations in discharge, temperature, food base, and species abundance) and by logistical problems associated with studying fishes in large, turbid rivers. The determination of limiting factors for rare fishes is further complicated because of limited life history information. Habitat use by the rare fishes may only reflect temporary, seasonal, or marginal habitat availability. Thus, caution must be exercised when determining habitat needs and limiting factors for fishes in decline, and professional biological judgment must be recognized as critical in data interpretation.

Some factors that may be limiting the distribution and abundance of rare fishes in the Yampa River are summarized in Table 6. This information is presented for consideration in future updates of the Sensitive Areas report (Upper Colorado River Basin Coordinating Committee 1984) and for aiding the Recovery Implementation Program (U.S. Fish and Wildlife Service 1987) for the Yampa River. Each species is discussed separately in the following sections. Although more information is available regarding habitat needs and limiting factors for the Colorado squawfish, we do not suggest that protection of a single species or a single life history stage will adequately protect all—we emphasize that each species is unique and has different requirements for survival.

Colorado Squawfish

An evaluation of factors limiting the distribution and abundance of Colorado squawfish in the Green River system is complex because of the wide range of habitat and flow conditions required by the different life history stages. High spring flows, in addition to increasing water temperatures, are necessary for the initiation of the spawning migration (Figs. 7 and 8). Decreasing flows and warming river temperatures in early and mid-summer are necessary for successful spawn and downstream transport of drifting larvae (Tyus et al. 1987; Fig. 11). Low flows in late summer and fall are correlated with availability of nursery habitat and young fish abundance and growth (Tyus et al. 1987; M. Pucherelli and R. Clark, written communication). A stable winter base-flow is necessary for maintenance of winter habitats (Wick and Hawkins 1989).

Adult

The potamodromous migrations and homing behavior of Colorado squawfish (Wick et al. 1983; Tyus and McAda 1984; Tyus 1985) from downstream Green River and upstream Yampa River to Yampa Canyon mandates protection of known migration routes, since feasibility of fish passage facilities for this species has yet to be demonstrated. We presume that blockage of these river sections by dams or water diversions will directly result in the local extinction of Colorado squawfish (Tyus 1984), as evidenced by the recent loss of 80 km of

Table 6. *Delineation of critical river reaches for rare and endangered Colorado River fishes in the Yampa River, with notes on potential limiting factors.*

Life history stage	Location (RK)[a]	Season	Potential limiting factors
		Colorado Squawfish	
Adult	0–224	All year	Spring peak flows; overbank flooding; seeps in spawning reaches; number of ripe females; angling or other incidental takes; siltation of spawning substrate; competition and predation with nonnative fishes; food availability; stream blockage; low flows late summer, fall, and winter; stability of winter flows.
Concentration	82–198	August–May	
Migration	0–224	May–August	
Spawning	6–51	June–August	
Larva	0–50	July–August	
Juvenile	0–224	All year	
		Humpback Chub	
Adult	0–90	All year	Spring peak flows; availability of shoreline eddy habitat and deep canyon habitat; competition and predation by nonnative fishes.
Concentration	6–64	All year	
Spawning	19–64	May–July	
Larva	0–64	May–July	
Juvenile	0–90	All year	
		Bonytail Chub	
Adult	0–16	All year	Factors unknown.
		Razorback Sucker	
Adult	0–21	All year	Spring peak flows; overbank flooding; number of reproducing adults; competition and predation by non-native fishes; lack of substantive recruitment to juvenile life history stage.
Spawning	0–6	April–June	
Larva	0–6	April–June	

[a] Numbers represent river kilometers (rounded) upstream from the mouth of the Yampa River.

occupied habitat in the White River due to blockage of access to overwintering areas (Martinez 1986). Localized water input at the spawning grounds may provide orientation cues for spawning Colorado squawfish, and thus, significance of groundwater and surface inflows in these areas, relative to survival of endangered fishes, should be further investigated.

The reproductive success of Colorado squawfish depends on a number of interdependent factors, including the number of spawning adults (particularly ripe females), river discharge, sediment load, temperature, and photoperiod. Condition and physiological readiness are also important factors. The presence of adult Colorado squawfish in inundated shorelines and lowlands during spring runoff suggests that such behavior, and associated feeding, may offset the large energy expenditure required for migration and spawning. Thus, natural overbank flooding in spring and the consequent increased availability of floodplain nutrients (Welcomme 1979) are important factors in physiological readiness of Colorado squawfish. The loss of successful reproduction in one or more years could effect a further decline of Colorado squawfish.

Colorado squawfish eggs are adhesive, and hatching success may depend on their attachment to substrate surfaces. Therefore, availability of cleaned cobble and boulder surfaces in spawning areas may be limiting, if flushing action from peak flows is significantly curtailed

by a reduction in spring runoff. A gradual decrease in summer flows, following spring scouring, with a concomitant decrease in sediment load, aids in preventing siltation of cobble bars. Thus, timing and duration of flushing flows must be evaluated as potential limiting factors for successful reproduction by Colorado squawfish.

Reproductive success of Colorado squawfish is believed to be limited by the low number of spawning adults. Captures of adult Colorado squawfish with lures and bait in the Yampa River (Saile 1986; U.S. Fish and Wildlife Service, unpublished data) suggest that large individuals are susceptible to angling pressure. Service records (Vernal, Utah) show that in some years up to 10% of the tagged Colorado squawfish are captured by anglers. Martinez (1986) also noted several instances of incidental captures in the White River. Thus, protection of adult Colorado squawfish should be encouraged because of the small number of juveniles, the long time required to attain maturity (> 5 years), and the susceptibility of large individuals to angling and other incidental captures.

Competition with introduced fishes for food or space and predation by nonnative forms are two factors that potentially limit survival of adult Colorado squawfish in the Yampa River. Capture of northern pike (*Esox lucius*) and channel catfish in habitats shared by adult Colorado squawfish (Wick et al. 1985; U.S. Fish and Wildlife Service, unpublished data) suggests that these nonnative predators may be competing with or preying on Colorado squawfish. Also, although Pimental et al. (1985) found that Colorado squawfish did not prefer channel catfish as prey, observations of channel catfish lodged in throats of adult Colorado squawfish (McAda 1983; Pimental et al. 1985; Wick et al. 1985) indicate that these introduced fish may adversely affect survival of Colorado squawfish.

Flow fluctuations in winter have the potential for disturbing preferred winter habitats, and the resultant movement patterns suggest that such disruptions may stress Colorado squawfish (Wick and Hawkins 1989). Thus, significant fluctuations in water surface level in winter are undesirable.

Larvae and Postlarvae

Factors potentially limiting the distribution and abundance of young Colorado squawfish in the Yampa River include the alteration of natural flow and temperature patterns and alteration of natural sediment and nutrient loads. Such alterations may negatively affect availability (quality and quantity) of critical nursery habitat in the Green River. In addition, proliferation of nonnative competitors and predators is considered limiting.

Mortality of drifting larvae is directly related to flow, river temperature, availability of backwater habitat, and predator load. Young Colorado squawfish are routinely collected in isolated pools in the Green River system (U.S. Fish and Wildlife Service, unpublished data). These pools form when decreasing flows strand water from the main channel. Natural fluctuations in river level usually make this a gradual process and allow entrapped fish an escape route. However, abrupt fluctuations in river level, as is characteristic of some regulated systems, could increase mortality of small fishes by cutting off escape routes and thereby increasing potential for competitive interactions and exposure to terrestrial predation. Herons (Ardeidae), raccoons (*Procyon lotor*), garter snakes (*Thamnophis* sp.), and other animals have been observed feeding on fishes trapped in isolated pools (Erman and Leidy 1975; U.S. Fish and Wildlife Service, unpublished data).

Effects of competition and predation by introduced fishes on growth and survival of young Colorado squawfish has yet to be adequately assessed, but the common use of backwater habitats and foods by young Colorado squawfish and other small introduced fish species (Jacobi and Jacobi 1982; McAda and Tyus 1984; U.S. Fish and Wildlife Service, unpublished data) indicates the potential for significant interspecific interaction. Karp and Tyus (in press) suggest that growth and survival of young Colorado squawfish may be adversely affected by introduced green sunfish (*Lepomis cyanellus*), red shiner (*Notropis lutrensis*), and fathead minnow (*Pimephales promelas*), particularly when increases or decreases in river level reduce the availability of quality backwater habitat.

There is some indication that abundance of nonnative fishes may be decreased by periods of high flows, whereas native species seem to be little affected (Haynes and Muth 1984; Minckley and Meffe 1987; T. Nesler, written communication). These preliminary relations support the hypothesis that native fishes exhibit greater tolerance to fluctuating flow regimens.

Late summer and fall are critical periods for growth and survival of young Colorado squawfish, and flows in the Green River system at this time are historically and predictably low. Tyus et al. (1987) noted that abundance and growth of young Colorado squawfish in the Green River was negatively correlated with late summer and fall flows ($r = -0.73, P < 0.06$ for abundance; $r = -0.88, P < 0.01$ for growth). During late summer and fall, catch and growth were highest in 1979 and 1980, when discharge ranged from 45.28 to 53.77 m^3/s at Jensen, Utah, and lowest in 1983 and 1984, when discharge ranged from 84.9 to 118.86 m^3/s (Tyus et al. 1987). In 1983 and 1984, unusually high releases from Flaming Gorge Dam in late summer and fall inundated backwater nursery areas, and survivorship of young Colorado squawfish was low. These relations suggest that flows optimizing growth and survival of small

Colorado squawfish vary with time of year, and that both reproduction and recruitment to the juvenile stage are highest in years when hydrographs approximate natural flow conditions. This presumably is related to the availability of nursery backwater habitat in fall.

Aerial photography was used to evaluate the effect of seven test flows on availability of backwater habitat in late summer and fall 1987 at four sites (Island Park, Jensen, Ouray, Sand Wash) in the upper Green River (M. Pucherelli and R. Clark, written communication). It was found that the greatest amount of backwater habitat resulted when flows ranged from 31.15 to 50.17 m^3/s, and the least amount of backwater habitat was present at flows of 68.57 and 148.85 m^3/s. Averaging the Jensen, Ouray, and Sand Wash sites (i.e., the upper Green River concentration area for young Colorado squawfish drifting out of the Yampa River), area of backwater habitat was greatest with flows of 50.17 and 47.74 m^3/s, and number of backwater habitats was maximized at 47.74 m^3/s. These relations support the biological information and emphasize that young Colorado squawfish need low flows in late summer and fall.

Juvenile

Factors limiting the distribution and abundance of juvenile Colorado squawfish are difficult to assess because there is little information available regarding their habitat requirements. Stream blockage is viewed as limiting because upstream movement of juveniles is necessary to maintain adult populations.

Evidence of predation by nonnative fishes in both artificial and natural environments suggests that this factor limits the survival of juvenile Colorado squawfish. Hendrickson and Brooks (1987) noted predation by yellow bullhead (*Ictalurus natalis*) and largemouth bass (*Micropterus salmoides*) on young Colorado squawfish stocked into the Verde River, Arizona. Osmundson (1987) noted predation by largemouth bass, green sunfish, black crappie (*Pomoxis nigromaculatus*), and black bullhead (*Ictalurus melas*) on young Colorado squawfish in gravel pits near the Colorado River, Colorado, and indicated that predation by channel catfish may also have occurred. In addition, Coon (1965) reported channel catfish predation on Colorado squawfish in the Dolores River. Flow regimens and other conditions that may aid the proliferation of these nonnative predators must be identified and, if possible, avoided.

Humpback Chub

Spring peak flows are important to reproductive success of the humpback chub, because spawning occurs in shoreline eddy habitat shortly after this period. Availability of these habitats is greatest during spring runoff and lessens thereafter with decreasing summer flows (Karp and Tyus 1989). Loss or reduction of spring runoff could reduce availability of spawning habitat and thus adversely affect humpback chub reproduction. Habitat alteration may also promote hybridization with other species (Valdez and Clemmer 1982). Flow reductions and decreased temperatures have been implicated as factors curtailing successful spawn and increasing competition in the Colorado River (Kaeding and Zimmerman 1983).

Humpback chubs and channel catfish may be competing for food or quality microhabitat as suggested by capture of both species with baits in the same eddy habitats in the Yampa River (Tyus and Minckley 1988; Karp and Tyus 1989). The high number of channel catfish in preferred humpback chub spawning habitat (30% of the catch in 1987 and 1988; Karp and Tyus 1989) suggests that this omnivorous introduced species may adversely affect reproductive success of the humpback chub in the Yampa Canyon. In addition, the presence of bite marks on humpback and roundtail chubs may be due to attempted predation by channel catfish (Kaeding and Zimmerman 1983; Karp and Tyus 1989; C. O. Minckley, personal communication). W. L. Minckley (personal communication) also noted humpback chub remains in stomachs of channel catfish captured in the Little Colorado River. Flows or other conditions (e.g., temperature; Tyus and Nikirk, in review) which may favor growth of channel catfish in the Green River basin should be determined and avoided.

Humpback chubs predominantly use canyon habitat (Fig. 4) and availability of such habitat could be adversely affected by alteration of the natural flow cycle of the Yampa River (Fig. 1).

Bonytail Chub

Bonytail chubs were never reported as abundant in the Yampa River and a decline is not indicated in that system. However, in the Echo Park area, bonytail chubs have apparently declined, possibly due to flow and temperature changes resulting from closure of Flaming Gorge Dam. A similar pattern has been noted in the Colorado River downstream from Glen Canyon Dam (Utah State Department of Fish and Game 1964, 1969). Although the preimpoundment poisoning of riverine habitat in the upper Green River in 1962 has been implicated in the decline of the bonytail chub in that system, fish collections in DNM before and after the poisoning (Binns et al. 1963; Vanicek and Kramer 1969; Vanicek et al. 1970) suggested that the downstream extent of the poison was not a factor in the almost total extirpation of the species from the Echo Park area. Current negotiations between the Fish and Wildlife Service and Bureau of Reclamation regarding management of Flaming Gorge Dam operations for rare fishes may improve the future of the bonytail chub in the

Green River system, especially if population augmentation is attempted.

Razorback Sucker

Adult razorback suckers in the Green River basin are old individuals (Tyus 1987; Lanigan and Tyus 1989; U.S. Fish and Wildlife Service, unpublished data), and the small number of reproducing razorback suckers is considered limiting. Razorback suckers spawn on the ascending limb of the hydrograph in the Green River basin; therefore, the interrelation of high spring flows, warming temperatures, and other factors are important for successful reproduction in this species.

The apparent lack of widespread recruitment in this species has been attributed to habitat alteration, such as lower water temperatures (Marsh 1985) and predation by introduced common carp (*Cyprinus carpio*), green sunfish, and other nonnative fishes (Minckley 1983; Tyus 1987; Marsh and Langhorst 1988; Marsh and Minckley 1989). Brooks et al. (1985) documented significant predation of stocked larval and fingerling-size razorback suckers by channel catfish and flathead catfish (*Pylodictis olivaris*). Predation by nonnative fishes is believed to be a serious threat to the survival of razorback suckers and is a consideration in recovery efforts for this species. The absence of young fish in the Green River basin population may also be linked with the reduced availability of inundated shorelines due to curtailment of spring flooding following closure of Flaming Gorge Dam. The introduction of young fish (from sex products taken from wild fish captured on nearby Green River spawning grounds and reared at Ouray National Wildlife Refuge) may ultimately result in natural recruitment if the number of spawning adults—and consequently the number of young—is increased.

Conclusions and Recommendations

The Yampa and Green rivers constitute the most important riverine system for the maintenance and recovery of rare Colorado River fishes. Flows of the Yampa River are singularly important for providing a natural shape to the hydrograph of the mainstream Green River and thereby mitigating possible adverse effects of flow regulation on the native fish fauna. Flows of the Yampa River, particularly spring runoff, may also enhance usable rare fish habitat by inhibiting the invasion and proliferation of introduced fishes that evolved in more mesic environments. As indicated in previous discussions, the Colorado squawfish and razorback sucker depend on habitats in the Yampa and Green rivers for fulfillment of various life history requirements. Therefore, these two river basins must be considered as a single ecosystem when determining the needs of indigenous rare fishes.

The Green River basin supports the largest numbers of Colorado squawfish (Tyus 1989) and razorback suckers (Lanigan and Tyus 1989) in native riverine habitats. The humpback chub is self-sustaining in the Yampa River and represents one of few remaining extant populations of this species. The persistence of native fishes in the Yampa River indicates that habitat conditions are suitable for their survival, despite the proliferation of many nonnative fishes. Population augmentation and study of razorback suckers and bonytail chubs in the upper Green River are proceeding and new information will hopefully aid in their recovery.

Flow needs of the rare fishes in the Yampa River are determined by many factors, including time of year, life history stage, and associated species. Reproductive activities of the Colorado squawfish, razorback sucker, and humpback chub in the Yampa River are closely associated with spring runoff (Fig. 15). Alteration of this hydrologic event may affect initiation of Colorado squawfish migration and spawning of Colorado squawfish, humpback chubs, razorback suckers, and other native fishes. Maintenance of low, stable flows in late summer and fall is necessary for growth and survival of young Colorado squawfish and presumably young of the other rare native fishes (Fig. 15). In addition, stable flows through ice breakup are important to overwinter survival of young and adults. Abrupt fluctuations in water level from late summer to spring could strand Colorado squawfish (larvae and adults) and presumably other native fishes. The relations shown in Fig. 15 indicate that the natural flow events characterizing the

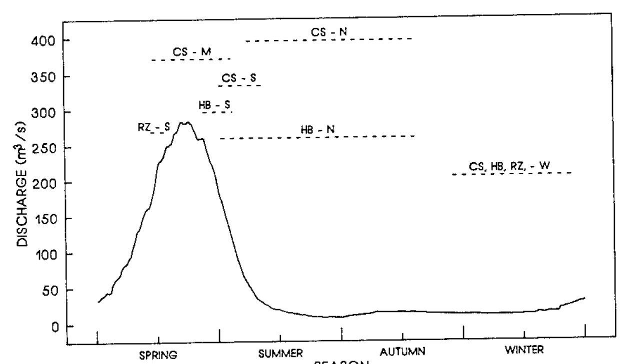

Fig. 15. Conceptual relation between Yampa River annual distribution hydrograph (1922–87 average) and timing of some life history events of Colorado squawfish, razorback sucker, and humpback chub. (Spring, 21 March–21 June; summer, 22 June–22 September; autumn, 23 September–21 December; winter, 22 December–20 March. CS = Colorado squawfish, HB = humpback chub, RZ = razorback sucker, M = migration, S = spawning, N = nursery, W = winter.)

Yampa River hydrograph should be protected as one effort toward recovery of the rare indigenous fishes.

We recommend that the Yampa River be given highest priority for water rights acquisition in the upper Colorado River basin. Further efforts to coordinate Green River flows (by operation of Flaming Gorge Dam) with timing of Yampa River flows are needed for recovery of the rare Colorado River fishes in the Green River basin. The following summaries highlight the flow events we consider to be important toward recovery of the rare Colorado River fishes in the Green River basin. These are presented by species and time of year.

Colorado Squawfish

Spring

Migration signals the onset of the reproductive cycle in Colorado squawfish, and we consider migration cues (e.g., high spring flows, increasing river temperatures, possible chemical inputs from flooded land) important to maintain successful reproduction. Duration and timing of spring runoff must be further evaluated with these needs in mind. Migration routes must be protected and barriers discouraged.

Summer

Spawning and egg deposition occur in association with declining flows, decreasing sediment transport, and increasing temperatures. Relations between these and other variables (e.g., type of water year) and spawning should be further evaluated with respect to low-, average-, and high-water years. The gradual decline of summer flows following spring scouring maintains natural sediment transport equilibria, prevents siltation of spawning substrate, aids downstream drift of larvae, and creates productive nursery areas.

Fall

Flows maximizing backwater habitat (quantity and quality) in the upper Green River should be determined using both the Yampa and Green rivers. Unusually high flows in late summer and fall reduce availability of nursery habitat for young Colorado squawfish.

Winter

Stable flows reduce ice scouring of shoreline habitats that are used by overwintering adults and young. In the event that flow quantifications through ice cover are not feasible, an alternative is to provide best conditions observed during the 1986–88 winter habitat study (Wick and Hawkins 1989) or subsequent studies.

Humpback Chub

Spring

Spawning of humpback chubs occurs shortly after highest spring discharge. Relations between these events should be further evaluated with consideration of availability of shoreline eddy habitat. The relation between spring flows and abundance of channel catfish should be evaluated.

Summer–winter

Habitat use and flow needs of the humpback chub during late summer and winter are not well understood, but minimum flows necessary for maintenance of riverine, canyon-bound habitat should be determined for dry, average, and wet years. Conditions favoring reproduction and growth of channel catfish should be identified and avoided because of possible negative interactions of these species.

Bonytail Chub

Studies are in progress to evaluate habitat use and needs of this species. Results of reintroduction efforts should be evaluated with respect to the current Yampa River hydrograph.

Razorback Sucker

Spring

Spawning of the razorback sucker occurs with increasing flows associated with highest spring runoff. Curtailment of spring runoff in the mainstream Green River may be associated with loss of recruitment to the juvenile stage. Relations between these events should be further evaluated with consideration of larval distribution, habitat use, and abundance in the Green River. Flooding of bottom-land during spring runoff may be beneficial to adults and important for dispersal and rearing of young. Influence of Yampa River flows on razorback sucker spawn in the Green River should be more fully evaluated.

Summer–winter

Little is known of habitat needs of the razorback sucker during this period. Thus, low, stable flows (natural condition) should be maintained until additional information is available.

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Appendix. Conversions from Metric system to English system.

kilometer (km)	× 0.625 = miles
meter (m)	× 3.281 = feet
cubic meter per second (m^3/s)	× 35.335 = cubic feet per second (ft^3/s)

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15. Supplementary Notes

16. Abstract (Limit: 200 words)

In the Yampa River, stream habitat needs and life history requirements of Colorado squawfish (Ptychocheilus lucius), humpback chub (Gila cypha), razorback sucker (Xyrauchen texanus), and other native Colorado River fishes are presently maintained by flow regimens approximating natural conditions. Yampa River flows are also important in reducing adverse water management practices in the downstream Green River. Management for recovery of endangered fishes in the Yampa River will require specific flows to provide seasonal requirements at different locations: high spring flows associated with the initiation of Colorado squawfish spawning migrations, humpback chub and razorback sucker spawning, and maintenance of spawning bars and eddy habitats; descending summer flows associated with Colorado squawfish spawning, downstream transport of larvae, and creation of nursery habitat; stable winter flows to remove the threat of ice damage to shoreline areas used by many species. Acquisition of Yampa River water rights may be the decisive factor in conservation of endangered fish species in the Green River basin.

17. Document Analysis a. Descriptors

Endangered species, rare and endangered fishes, Colorado River fishes, Colorado squawfish, humpback chub, razorback sucker, bonytail chub, streamflow habitat use

b. Identifiers/Open-Ended Terms

Colorado River, Green River, Yampa River, habitat, stream, western States

c. COSATI Field/Group

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